GOING THROUGH THE MOTIONS: THE IMPACTS OF FREQUENT FIRES AND GRAZING PRESSURE ON REPRODUCTION BY MONTANE GRASSLAND BIRDS

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DECLARATION

This thesis describe original research undertaken towards a PhD. Degree at the Percy FitzPatrick, University of Cape Town, which has not been submitted in any form towards degree at any other University. I submit it as my own work and have acknowledged all assistance I received.

signature removed

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"Happiness comes not from having much to live on but having much to live for."

William Arthur Ward

ABSTRACT

Land management practices have been implicated as a cause for the decline of many grassland-nesting birds across the globe. While this effect has motivated extensive research and conservation in the developed northern hemisphere, it remains poorly addressed in southern hemisphere. Between 1998 and 2001 I examined the effect of fire frequency and grazing intensity on the density, breeding biology and nesting success of several grassland bird species that breed in the high altitude grasslands of Wakkerstroom, South Africa.

I established study plots in heavily grazed and annually burned, lightly grazed and annually burned, and lightly grazed and biennially burned plots. These represent the most frequently used grassland management regimes in this region. Independent analysis of all study species showed that daily nesting success was higher under light than heavy grazing. Similarly, nesting success was higher under biennial burning when compared to annual burning. Nest predation was the major cause of nest failure during all three years for all species. The likelihood of nest predation clearly depended upon foliage in the immediate vicinity of the nest and vegetation within 10 m radius of the nest (the nest patch). In general, variables important in discriminating between successful and depredated nests across all species were directly related to vegetation cover, density and horizontal heterogeneity.

I also examined microhabitat choices, the form of natural selection and the adaptiveness of preferences in four coexisting grassland bird species (Yellow-breasted Pipit *Hemimacronyx chloris*, Grassveld Pipit *Anthus cinamomerous*, Orange-throated Longclaw *Macrony capensis*, and Ayre's Cisticola *Cisticola ayressii*). Breeding birds selected nest patches non-randomly and this differed between species. Comparison of vegetation features at successful and unsuccessful nests supported the idea that nesting success is a strong selective force on habitat choice. Nest success was higher in preferred than non-preferred habitat for all the four species, suggesting that preferences were adaptive. Estimation of fitness functions relating fitness of individuals to critical habitat features suggests that natural selection might favour preferences for specific habitat features.

Although food abundance and thus amount of food available to populations of breeding birds significantly differed between management regimes, the study yielded no evidence for an effect of management-mediated food abundance on feeding rate, nestling provisioning rates, nestling growth rates, body condition, nest attentiveness and brooding effort. My results suggest that the food availability alone may not be the most important

factor influencing the production of offspring. Instead, nest predation appeared to be of major importance in this system.

Theoretically, nest predation increases with activity at nests, and predation rates should peak during the nestling stage when birds are feeding young. I tested this hypothesis using three ecologically similar grassland bird species (Yellow-breasted Pipit, Orange-throated Longclaw, and Grassveld Pipit). Parental activity was indeed greater during the nestling than incubation stage. Nest predation, however, did not increase with parental activity between these stages in all three study species. I conducted an experiment that controlled for parental activity (by reusing natural nests of the study species with artificial clutches) in order to test for nest-site effects. Nests that had a high risk of predation when used by active parents had a correspondingly high risk of predation when the same nests were re-used with artificial clutches (i.e. when controlling for parental activity). This result supports the notion that variation in nest-site quality often affects nest predation risk, and such effects could mask parental activity effects on nest predation. Once-nest site effects were accounted for, nest predation showed a positive increase with parental activity during the nestling stage within and across species.

Collectively, the chapters of this thesis help to diagnose the causes and underlying mechanisms of grassland bird population decreases, and help to identify the most effective conservation actions. In short, conservation effort for grassland species should be directed at ensuring that their preferred critical nesting habitat is managed appropriately. I propose that current intensive grazing pressure and periodic burning should be relaxed by reducing stocking rates and burning less frequently to benefit grassland bird species. Ideally, grasslands should be burned biennially and grazed moderately.

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1

GENERAL INTRODUCTION

Vegetation types having similar vegetation structure, sharing important plant species and having similar ecological processes constitute a biome (Low and Rebelo 1996). Different grassland vegetation types (also known in South Africa as grassveld) are distinguished as components of the southern African grassland biome. This biome is located primarily on the central plateau of South Africa, and the inland areas of KwaZulu Natal and the Eastern Cape (Low and Rebelo 1996). Topography is mainly flat and rolling with some steeply slopes on the escarpment (Low and Rebelo 1996). The South African grassland biome covers 349 174 km^2 (Cowling et al., 1997), accounting for 16.5 % of the South African land surface area. Despite hosting a remarkable and unique fauna and flora (see Siegfried 1989 for a comparision with other biomes), little appreciation has been given to this biome as having any biotic resources worth of conservation (Tarboton 1997b).

In South Africa, as elsewhere in the world (Keith *et al.* 1992), the plight of grassland is relatively under-appreciated. For example, only 2% of the grassland biome in South Africa is conserved in the formal protected area estate, compared to 78% of the forest biome (Siegfried 1992). Grasslands are under considerable threat from massive transformation. Sixty-five percent of the pristine grassland biome is already transformed by cultivation, afforestation, industrialisation, mining and urbanisation (Scharfetter 1987, Allan *et al.* 1997; Tarboton 1997b; Low and Rebelo 1996, Cowling *et al.* 1997). The grassland biome, in particular, is also subjected to rapid retreat due to degradation by bad management practices (Brooke 1984, Clancey 1985, Kruger et al, 1995, O'Connor and Bredenkamp 1997, Tarboton 1997a). Being the most economically developed country on the continent, South Africa's biological resources, and particularly its highland grasslands, have been heavily impacted by man (IUCN 1990).

The Southern African grassland biome comprises a high incidence of fauna and flora (Barnes 1998). Three hundred and fifty (350) bird species are found in the grassland biome (Harrison *et al.*, 1994), of which about 40% are considered to be obligate or true grassland birds species (i.e. exclusively adapted to and entirely dependent on grassland habitats). Twenty-five (25) of the latter species are of conservation concern (Barnes 2000). Ten (10) of the true grassland birds species are endemic to the South African grassland (Brooke 1984, Colar *et al.* 1994, Barnes 1998, 2000). These include the Yellow-breasted pipit *Hemimacronyx* (*Anthus*) *chloris*, Bald Ibis *Geronticus calvus*, Blue Korhaan

Eupodotis caerulescens, Rudd's Lark *Heteromirafra ruddi*, Botha's Lark *Spizocorys fringillas*, Buff-streaked Chat *Oenanthe bifasciata*, Orange-breasted Rockjumper *Chaetops auruntius*, Drakensberg Prinia *Prinia hypoxantha*, Mountain Pipit *Anthus hoeschii* and Drakensberg Siskin *Sernus symonsi*. Of these, Rudd's Lark is considered to be globally critically endangered and Bald Ibis, Botha's Lark and Yellow-breasted Pipit as globally vulnerable (Birdlife International 2000). The former category implies that a species is facing an extremely high risk of extinction in the wild in the immediate future. Although this grassland habitat and its bird populations are thought to be in decline (Clancey 1985, Keith *et al.* 1992), remarkably little is known about the status of its birds, their ecology, and how they are affected by current land-use changes (but see Hockey *et al.* 1988). The biome also hosts many other fauna including a wide diversity of grasshoppers, (Dirsh 1956, Brown 1962, Armstroom and Hensbergen 1997), butterflies (Pringle *et al.* 1994), reptiles, amphibians, molluscs, and other community (Barnes 1998). Floristically, the grassland biome comprises a centre for plant endemism and diversity for many large genera, with an estimated 3788 species in the core region, or 82 species per km^2 (Gibbs 1987, Matthews *et al.* 1993). High rates of endemism are likely to be found among other taxa as well (see Barnes 1998).

History of the South African grasslands

The habitat at any point is, in part, a function of its history, extent, and trajectory of change at multiple spatial and temporal scales (Scott *et al.*1997). Evidence from pollen macrofossils from several sites in South Africa suggests that grasses have essentially been in place throughout the Holocene, and that they were often widespread during the Pleistocene (Scott *et al.*1997). Although there is evidence of some movements of boundaries within the grassland biome, data from different sites in South Africa suggest that the grassland biome occupied roughly the same area during the Holocene as it does today (Scott *et al.*1997).

Some human impacts on South African grassland ecosystems possibly were started by early Iron-Age farmers in about 250 AD (Feely 1979, 1987). Prior to the introduction of modern farming and livestock, hunting and gathering was the only land use on the South African grassland and savannah (Downing 1978). Until 2000 years ago, the native San (Bushmen) and Khoikhoi (Hottentots) people occurred at low density and had little impact on the grasslands (Downing 1978). In their time, these people hunted wild animals and

gathered wild roots and herbs amid teeming herds of buffalo, wildebeest, blesbok, and other herbivores that roamed the huge expanse of the grasslands. These wild herbivores were nomadic or migratory, occurring infrequently at high density for short periods. Although it is not very well known how often natural fires occurred, presumably they did not occur as often as the present prescribed burning which has increased burning of grasslands both in scale and extent (Downing 1978).

The arrival of the Nguni speaking people some two thousands years ago showed the start of a gradual change in the grasslands (Feely 1987, Downing 1978). However, the arrival of European whites from around 1652 accelerated the change (Downing 1978). The arrival of the European whites also opened the region to thousands of traders and commercial settlers and hunters. Extensive populations of wild ungulates were hunted on the grassland until they were virtually eliminated towards the latter part of the 19th century. With the extermination of these wild herbivore populations, the grasslands were settled by farmers who kept sedentary herds of livestock, or who cultivated crops (Feely 1987, Downing 1978).

With development of increasingly modern farming techniques and farm machinery, the period between 1850 to 1950 resulted in the conversion of thousands of hectares of native grassland to cultivated crops like maize (today 3.5 million ha of maize are planted each year), wheat, cabbages, fruit and plantation of forests. The discovery of gold (Witwatersrand and Northern Free State), diamond (Northwest) and coal (Mpumalanga highland grassland and Northern KwaZulu-Natal) in the early 19th century transformed parts of the grassland to mining fields (Petersen *et al.* 1985, Macdonald 1989, Tarboton 1997b) and associated industries (Preston-Whyte and Tyson 1988, Tyson *et al.* 1988). Urban cities and towns like Johannesburg (Gauteng), Bloemfontein, Klerksdorp, Newcastle, Witbank, and Welkom are today situated within the grassland biome.

Grasslands have diminished as intensive agriculture, afforestation, mining, excessive burning, and the sustained pressure of intensive grazing by livestock have steadily replaced the pristine, native highland grasslands (e.g. see Downing 1978, O'Connor and Bredenkamp 1997). Most of the fauna that was once common in this region is locally extinct, rare or endangered, and the species that survive today do so in dwindling numbers in the small, fragmented grassland remnants.

Many birds inhabiting grasslands have undergone significant population declines throughout the world (Robbins *et al.*, 1989, Goriup 1988, Knopf 1997, Bennun and Njoroge

1999, Muchai *et al.* 2002) and seem to be showing the most general and extensive population declines of any group of birds (Martin 1992a). In the South African highland grasslands, for example, numbers of Yellow-breasted Pipit (Globally vulnerable) and Rudd's Lark (Globally critically endangered), have declined drastically throughout much of their breeding range over recent years almost without being noticed (Tarboton 1997b, Hockey *et al.* 1988). In many cases, the decline comprises groups of species that are ecologically similar, suggesting general underlying causes for these declines (see Askins 1993, Caughley 1994). In South Africa, intensified grazing by livestock and unnatural fire regimes have been suggested as the main causes of such declines (Allan *et al.* 1997, Tarboton 1997a).

Livestock grazing is a dominant land use in the high-altitude grasslands of South Africa.

Although periodic fire and grazing have both been used extensively as management tools since the 1930s (Mentis 1981, Macdonald 1989), the ecological effects of these management practices on the reproduction of birds in the South African grasslands remain poorly understood.

Fire and grazing as grassland management tools

Semi-natural and natural grasslands are dynamic systems dependent on regular disturbance such as grazing or fire for maintaining vegetation structure (Knopf and Samson 1997). Farmers in the Wakkerstroom study area burn immediately after the onset of summer rains. Both periodic fire and grazing have historically been prominent features of natural ecology of the grasslands, here in South Africa and elsewhere, and both continue to be important ecological processes today (O'Connor and Bredenkamp, 1997, Knopf and Samson 1997). The role of fire (Leopold *et al.* 1963, Wright and Bailey 1982, Wade and Lundsford 1990) and grazing (Michunas *et al.* 1988) in maintaining diversity in ecosystems, including grassland systems is well known as well as how it affects livestock production (Mentis 1981, Macdonald 1989, O'Connor and Bredenkamp 1997). However, the indirect impacts of fire and grazing on other biota are not known.

Grazing climax grasslands are maintained by grazing (Tainton 1981). Grazing is used as a management tool to remove accumulated material left over from previous seasons, to stimulate new growth, and to control encroachment of undesirable plants. Grazing climax grasslands are sweet (i.e. lower fibre content and maintain their nutrient in

the leaves throughout the whole year) and do not deteriorate if under-utilised. There is therefore no real need to remove accumulated material by means other than grazing (Tainton 1981). Overgrazing tends to increase the proportion of sour grass. Thus careful management of grassland is required to maintain the abundance of sweet grass. Sweet grasses predominate at lower rainfall (below 625 mm). These grasslands do not withstand frequent fire and regular burning has a negative effect (Tainton 1981). Despite this, most landowners burn these grassland annually.

Fire climax grasslands are maintained by fire (Tainton 1981). Fire is mainly used as a management tool to burn off unpalatable growth left over from previous seasons, to stimulate new growth, to control encroachment of undesirable vegetation, and to control ticks and other parasites (Mentis 1981, O'Connor and Bredenkamp 1997). Fire climax grasslands are sour (i.e. lower fibre content and tend to withdraw their nutrients from the leaves during winter so that they are unpalatable in the mature growth stage). This grassland deteriorates if it is left unutilised even for short periods, thus requiring frequent burns (Tainton 1981). However, since it is grazed throughout summer, accumulation of litter generally does not occur. Thus frequent burning is not justified. Although optimal burning frequency is supposed to vary according to the rate of litter accumulation (Stuart-Hill and Mentis 1982), most farmers within these grasslands burn their farms annually irrespective of litter accumulation (Tainton 1981). As a result, over 90 % of the grasslands are burned annually.

Nest predation, food limitation and their effect on avian life history parameters

One possible indirect link between grassland management practices and grassland bird population declines could be through reproductive dysfunction through reduced nesting success.

Alteration of habitats by management practices is likely to affect nesting success through removal or reduction of nesting substrates which conceal nests from nest predators (e.g. see Ammon and Stacey 1997). Yet, few studies have examined relationships between nesting success of grassland birds and grassland management practices. Nest predation is the primary cause of reproductive failure for many passerine birds (Ricklefs 1969, Martin and Roper 1988), and is thought to be a critical factor shaping many aspects of avian reproductive biology, behaviour and a variety of life history strategies in birds (Skutch 1949, Lindern and Møller 1989, Kuleza 1990, Bosque and Bosque 1995, Martin *et al.*

2000a). Only a few studies have shown a relationship between nest predation and general habitat structure (Bowman and Harris 1980), nest-site habitat features (Martin and Roper 1988, Norment 1993), the behaviour of nesting birds (Cresswell 1997), and parental activity (Skutch 1949, Martin *et al.* 2000b).

Further, there are few documented examples of life history shifts induced by nest predation (Julliard *et al.* 1997). Nevertheless, the risk of nest predation may be a critical factor affecting clutch size (Skutch 1949, Perrins 1977, Ricklefs 1977, Martin *et al.* 2000a), nest site selection (Martin and Roper 1988, Møller 1988, Martin 1998), patterns of nest attentiveness (Martin and Ghalambor 1999) and patterns of parental effort (Skutch 1969, Martin 1992, Martin *et al.* 2000b). Empirical demonstration of the role of nest predation on avian life history is mostly lacking (Martin *et al.* 2000a), particularly in the tropics where predation is intense (Ricklefs 1969, Skutch 1976).

Population declines require immediate action, but such actions will be misguided if we are not managing the appropriate habitat features. Yet, proper identification of critical habitat features influencing fitness, which are necessary for effective management effort, is still lacking. When birds settle in habitats and select nesting patches, they are believed to do so non-randomly (Fretwell 1972). However, it remains unclear as to why individuals are not randomly distributed across habitat types. Nest-site microhabitat choices are assumed to be adaptive such that fitness is greater in preferred than non-preferred microhabitats (Jaenike and Holt 1991). Although genetic variation for habitat selection is common, particularly in invertebrates (Kekick *et al.* 1980, Jaenike and Holt 1991), only few studies have attempted to test the genetic basis of habitat selection in birds in particular (Martin 1998), or vertebrates in general (Schluter 1988).

Grassland management regimes can change the diversity, dominance, cover and structure of grassland plant communities (e.g. see Milchnas *et al.* 1988, Bullock and Pakeman 1997, Van der Koppel *et al.* 1997, Dupré and Diekmann 2001). The defoliation of grassland by disturbance regimes (herbivory and fire) can potentially have positive or negative consequences for the various members of the food chain that live in the grassland (e.g. see Dickson 1981, Curry 1994). Availability of food is often considered to be the most important factor influencing the production of offspring and variation in life history traits of birds (Lack 1968, Roff 1992, Martin 1987; but see Ricklefs 1969, Martin 1995a). Nestling growth and survival are particularly sensitive to variation in food supply in several bird species (Rondenhouse and Holmes 1992). Further, low food availability can influence

schedules of parental care (Weathers and Sullivan 1989) and considerably constrain the amount of food delivered to nestlings (e.g. see Harris 1969, Quinney 1982). This in turn can influence nestling growth and body condition. Reduced availability of food, is also predicted to affect bird densities (e.g. see Milchnas), limit clutch size (Ruiz *et al.* 2000) and the number of breeding attempts (Martin 1987, 1993a, Rodenhouse 1986), thereby influencing breeding productivity.

The general trend in variation of life-history strategies among species has chiefly been attributed to trade-offs maximising lifetime reproductive output (e.g. Roff 1992). Although a variety of traits can be influenced by costs associated with local conditions, one trait that seems consistently modified is clutch size (Skutch 1949, Lima 1987, Martin 1988b). Despite the fact that clutch size is one of the traits showing close adjustments to local conditions (Lack 1968), the proximate mechanism by which clutch size is adjusted can vary. The evolution of clutch size has long been attributed to food (Lack 1948, Charnov and Krebs 1974), adult survival (Charlesworth 1994), environmental unpredictability (Stearns 1992), and nest predation (Slagsvold 1982, Martin 1995a, Julliard *et al.* 1997, Martin *et al.* 2000a). Skutch (1949) proposed that increased parental activity can proximately increase the risk of nest predation, which in turn constrains the rate at which parent birds can deliver food to young. This in turn constrains clutch size by limiting the number of young that parents can feed.

Approach and organization of the study

The study was conducted high altitude grasslands of Wakkerstroom, Mpumalanga province, South Africa. The study species included nine key grassland bird species, viz. Yellow-breasted Pipit *Hemimacronyx chloris* (YBP), Grassveld Pipit *Anthus cinamomerous* (GP), Orange-throated Longclaw *Macronyx capensis* (OTL), Ayres' Cisticola *Cisticola ayressii* (AC), Long-tailed Widow *Euplectes progne* (LTW), Common Quail *Coturnix coturnix* (CQ), Quail Finch *Ortygospiza atricollis* (QF), Rudd's Lark *Heteromirafra ruddi* (RL), and Red-capped Lark *Calandrella cinerea* (RCL). These were used as representative species to help in understanding the processes and mechanisms involved in the causes and effects of avian responses to management practices. In particular, the species were used to answer six key questions: (1) how do changes in plant diversity, dominance, cover and structure relate to various management practices; (2) how

are the populations of grassland birds species affected by grass species composition, grass cover, and vegetation structure; (3) how do various land uses and management practices affect the reproductive success of grassland birds; (4) how does grassland bird food (arthropod) abundance relate to different grazing intensity and fire frequency; (5) what are the effects of grassland management practices on parental care (food provisioning, brooding, breeding behaviour, and activity at nest); and (6) how do birds' health and body condition relate to grazing and burning management regimes?

The results of this study are presented as a sequence of discrete papers (Chapters 2-7). This approach allows quick communication of results, but eventually results in some repetition, particularly in the presentation of the methods used. When this thesis is read in a single sitting, this repetition is likely to become tedious and I apologize in advance for this. The synthesis (Chapter 8) paints the big picture of our understanding concerning the management of grasslands for the benefit of conservation-dependent birds.

Finally, I present my results of observer effects on nesting success as an appendix chapter (Appendix A).

2

Effects of burning and grazing management practices on the nesting success of grassland birds

Abstract.

Land management practices have been implicated as a cause for the decline of many grassland-nesting birds. One possible link between management practices and avian population decline could be a reduction in nesting success. I examined from 1998 through 2001 the effect of management practices on nesting vegetation and nesting success of the Yellow-breasted Pipit (vulnerable), Rudd's Lark (critically endangered) and other grassland birds that breed in the high altitude grasslands of Wakkerstroom, South Africa. Study plots were set out in heavily grazed and annually burned (H+B), lightly grazed and annually burned (L+A), and lightly grazed and biennially burned plots (L+B). These represent the most frequently used grassland management regimes. Vegetation cover, structure and heterogeneity were lowest under heavy grazing (H+A), intermediate under light grazing (L+A), and highest under biennial burning (L+B). Only a few Grassveld Pipits, Red-capped Larks and one Rudd's Lark ever bred in heavily grazed plots. Independent analysis of all study species showed that daily nesting success was higher on lightly grazed than heavily grazed plots. Similarly, nesting success was higher under biennial burning than under annual burning. Livestock grazing and burning clearly affects availability and quality of nesting substrates for grassland birds thus increasing nest predation. Nest predation is one of the potential causal links between management regimes and population declines in grassland birds and this is in accordance with other studies. The poor nesting success of study species in intensively grazed and frequently burned grasslands suggests that conservation effort for grassland species should be directed at ensuring that their preferred critical nesting habitat is managed appropriately. Ideally, grasslands should be burned biennially and grazed only moderately.

Key words: Grassland birds, livestock grazing, burning, nest success, rarity, population declines.

INTRODUCTION

Many grassland birds have undergone significant population declines throughout the world (Robbins *et al.* 1989, Goriup 1988, Green 1995, Knopf 1997, Bennun and Njoroge 1999) and seem to be showing the most general and extensive population declines of any group of birds (Martin 1992). In the South African highland grassland biome, for example, numbers of Yellow-breasted Pipit (Globally vulnerable) and Rudd's Lark (Globally critically endangered) (BirdLife International 2000), have declined drastically throughout much of their breeding range over recent years almost without being noticed (Tarboton 1997a, Hockey *et al.* 1988). In many cases, the decline comprises groups of species inhabiting the same habitat and/or having similar ecological requirements, signifying that there may be some general underlying causes for these population declines (also see Askins 1993). Many plausible causes have been mentioned in the declining-population paradigm (e.g. see Caughley, 1994) worldwide and regionally. In South Africa, changing land-use and inappropriate management practices have been implicated as the primary causes behind the observed patterns in population declines of grassland bird species (Allan *et al.* 1997, Tarboton 1997b). Although periodic fire and grazing have both been extensively used as management tools in the South African highland grasslands since the 1930s (Mentis 1981, Macdonald 1989), the ecological effects of these management practices on grassland birds' habitats and avian population viability remain poorly understood. One possible indirect link between grassland management practices and grassland bird population declines could be reproductive dysfunction through reduced nesting success. Alteration of characteristics of habitats by agricultural land-use should affect nesting success through the removal or reduction of nesting substrates (e.g. see Ammon and Stacey 1997).

Proper and reliable diagnosis of the causes of population declines is critical for effective management and in deciding priorities for of conservation action (e.g. see Pimm *et al.* 1988, Martin 1993b, Green 1995, Martin 1995b).

In this paper I conduct controlled field experiments to test the hypothesis that nesting success (egg survival, and nestling survival) of South African high altitude grassland birds varies in relation to grazing and burning management practices. First, I show that management regime affects vegetation characteristics. Second, I show that both livestock grazing and burning regime affect nesting success. Third, I partition causes of nest mortality into cause-specific components in order to understand the mechanisms that limit avian reproductive success. Fourth, I show that vegetation characteristic change with

season and that nest mortality decreases with an increase in vegetation structure, which provides improved concealment for nests.

Study species

My study focussed on eight ground-nesting grassland birds, viz. Yellow-breasted Pipit *Hemimacronyx* (*Anthus*) *chloris* (YBP), Grassveld Pipit *Anthus cinamomerous* (GP), Orange-throated Longclaw *Macronyx capensis* (OTL), Ayres' Cisticola *Cisticola ayressii* (AC), Long-tailed Widow *Euplectes progne* (LTW), Common Quail *Coturnix coturnix* (CQ), Quail Finch *Ortygospiza atricollis* (QF), Rudd's Lark *Heteromirafra ruddi* (RL), and Red-capped Lark *Calandrella cinerea* (RCL).

METHODS

Study area

The study was conducted in the high altitude grasslands of Wakkerstroom (centered at 27° 10' S, 30° 06' E) in Mpumalanga province, South Africa at 1800-2250 m A.S.L. from 1998-2001. The main land use in the Wakkerstroom district is large-scale livestock farming for beef. The district experiences a temperature climate with mild to warm summers, and cold and dry winters with occasional snow. Rain falls in summer at an average rate of between 700 mm and 1200 mm. Prescribed burning and grazing are used as management tools over the entire South African highland grassland biome. The highland grassland of Mpumalanga has been under considerable pressure from overgrazing since the 1930s (Downing 1978, Edwards 1981, Hockey *et al.* 1988). Also, although the optimal burning frequency is supposed to vary according to the rate of litter accumulation (Stuart-Hill and Mentis 1982), most farmers in Mpumalanga burn their farms annually irrespective of litter accumulation (Tainton 1981). As a result, over 90 % of the grassland get burned every year.

Experimental design

To examine effects of different grassland management practices on reproductive success, and to test the above hypothesis, I controlled for slope and aspect and selected plots representing three sets of management regimes, viz. (1) heavily grazed and annually burned (H+A); (2) lightly grazed and annually burned (L+A); and (3) lightly grazed and biennially burned (L+B). Six replicate treatment plots were used for each management regime. The

treatment plots (experimental units) were separated from others by at least 500m wide strips and were all within 10 km^2 of continuous grassland. All study plots were approximately 25 ha in size. Grazing intensity was defined as the number of large animal unit grazing in an area of one hectare (ha/LAU), or the grazing area allocated per each large animal units (LAU/ha). One LAU is equivalent to 1 cow (454 kg) or 5 sheep (Owen-Smith and Dankwerts 1997). Heavy grazing intensity was assumed to be > 3 LAU/ha while light grazing was < 1.5 LAU/ha. During the 1998/1999 breeding season, I controlled for burning and tested for effects of grazing (heavy versus light). During the 1999-2001 breeding season, I controlled for grazing and tested for effects of burning (annual versus biennial).

Field work

The study involved three major activities: (1) vegetation surveys across management regimes to determine how habitat variables related to management practices; (2) nest finding and monitoring natural nests to assess nesting success between species and across treatment plots; and (3) reuse of natural nests with artificial clutches (real and artificial eggs) to assess nesting success between species and between treatment plots for experimental clutches.

Assessment of vegetation differences between management regimes

Vegetation structure was surveyed three times for each treatment viz. at the start of the spring growing season, and two and four months latter. These surveys used techniques modified from Wiens and Rotenburry (1981). At 50-m intervals along each of the three 500 m long transects, I positioned myself at a random point, closed my eyes and turned several times before throwing a 1-m stick upwards. A 10-m tape was then laid out perpendicularly to the transect with the zero mark at the thick end of the stick. Vegetation was then sampled at 1-m intervals yielding 100 point samples of vegetation per transect (i.e. a total of 300 point samples per grassland plot). At each sampling point, a thin (6-mm diameter) rod was placed vertically through the vegetation to the ground, and the number of contacts ("hits") with plants within 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm and 60-100 cm heights intervals recorded. The plant species making contact with the rod at each 1-m interval of the tape, as well as litter depth was recorded. Bare ground or presence of rocks was noted when vegetation or litter was absent at the point of contact. The following 10 variables were then recorded: (1) percentage grass cover (%GCOV); (2) percentage herb

cover (%HCOV) (i.e. the percentage coverage of grasses and herbs was calculated as the frequency of occurrence of each type at all samples along each transect); (3) percentage total ground cover (%TGCOV) calculated as the proportion of all points not recording bare ground or rocks; (4) mean maximum vegetation height (MAXHGT) given by the maximum height of the rod recording contacts with vegetation; (5) mean horizontal foliage density (HIT0-10) calculated as the number of contacts of vegetation with the rod in the 0-10 cm height intervals; (6) mean vertical foliage density (TOTHITS) calculated as the mean total number of contacts over the entire height of the rod; (7) horizontal heterogeneity calculated using the coefficient of variation of the maximum height interval with hits (CVMAXHGT); (8) horizontal heterogeneity calculated using the coefficient of variation of the mean total number of contacts over the entire height of the rod (CVTOTHITS); (9) horizontal foliage diversity (HFD10) calculated using a heterogeneity index according to Wiens and Rotenberry (1981); and (10) vertical foliage diversity (VDF10) calculated using the Shannon diversity index.

Nest searches and monitoring

Study plots were searched for nests of all grassland bird species over the entire breeding season (October to April) during each of the three years of the study (1998-2001). Searching and locating of nests was done by dragging a 50m rope between two people to flush out birds from nests, or based on behavioural observation. Nest sites were marked (for relocation) with a stick or stone placed 10 m away from each nest. Nests were visited at one to five-day intervals to determine nest fate (success versus failure). Nests were considered successful only if one or more young fledged. When a nest failed, I determined the cause of failure as follows: (1) desertion, if nest failed due to abandonment after eggs were laid; (2) starvation, if nestlings were found dead or were absent after a marked retarded growth with no visible signs of illness or other causes of mortality; (3) trampling, if eggs or nestlings were found smashed inside the nest; (4) adult mortality, if an adult was found dead in or near nest or if the entire brood was found dead inside nest with no signs of predation or symptoms of disease; (5) weather, if the nestlings died after an extreme weather event or were flooded; and, (6) predation, if eggs or nestlings younger than fledgling age disappeared from the nest (with or without definite evidence of predation). Partial predation was assumed to have occurred when partial losses of eggs occurred, or if some of the nestlings disappeared with no prior signs of illness or starvation. Brood

parasitism (mainly by Cuckoofinch *Anomalospiza imberbis*) was only recorded in two Ayre's Cisticola nests. A conscious effort was made to minimize disturbance of breeding birds and their nests. To this end, gloves were used while handling nests and their contents. Human observer visitation to the nests, however, did not affect nest predation rates (see Appendix Chapter A).

DATA ANALYSIS

Assessment of vegetation differences across management regimes

Univariate comparisons of vegetation between management regimes involved one-way ANOVA (Sokal and Rohlf 1995, Zar 1984). Pairwise comparisons between grasslands were made for each vegetation variable using Wilcoxon two-sample tests. Overall differences between management regimes were analysed using stepwise logistic regression analysis. Stepwise discriminant function analysis (SDFA) was used to identify vegetation variables that differentiated between management regimes. The criterion for adding a variable from the model was $F = 2$ for the SDFA and, for adding a variable into the model, $\alpha = 0.1$ for the log-likelihood ratio statistic.

Daily Survival and nesting success

Nests were discovered at various stages of development. Daily nest mortality (DMR) was calculated using the Mayfield method (Mayfield 1961, 1975), which only uses information from the period during which a nest was under observation. These estimates consider any nest failure regardless of cause. I used the first day of egg laying (if the nest was found during the building stage) or the day the nest was found (if the nest was found after the first egg was laid) as the first day of observation. The mid-point between nest visits was used to estimate when critical events in the nesting cycle occurred. Half the number of days between subsequent visits over which a nest failed or fledged (although I did not extrapolate beyond the normal nesting period) was added to the previous number of days the nest survived to obtain the total exposure days (Mayfield 1961). I followed nests until fledging or failure. For each species, I calculated daily mortality as the number of failures divided by the total number of active nest observation days (exposure days). I calculated daily survival as (1 – daily mortality). I analyzed nest survival rates during the incubation period (period from the date the first egg was laid until hatching) and nestling period separately. Overall, daily nest survival (the probability of a nest surviving both the

incubation and nestling periods) was based on the pooled daily survival rates within each nesting period. I calculated standard errors of Mayfield's survival probabilities according to Johnson (1979) and variance of Mayfield's estimator according to Hensler and Nichols (1981).

Hypothesis testing was conducted using the Z-test for daily survival probability according to Hensler and Nichols (1981) and Program CONTRAST (Hines and Saucer1989) for multiple comparisons of daily nest survival. This program uses a χ^2–approach that is similar to ANOVA in order to control for experiment-wise error and adjust for Type I errors (Hines and Saucer 1989). I analyzed nest survival rates during the egg period (period from the date the first egg was laid until the hatching) and nestling period separately. Overall daily nest survival (the probability of a nest surviving both the incubation and nestling periods) was analyzed by pooling daily survival rates within each nesting period. I also grouped nests into those observed during early (October-November), mid (December-January) and late (February-April) season. Statistical analysis of nest success was limited to species with at least five nests in any particular management treatment. For each study species, I tested for all nests whether nesting success differed between years, between season, and among management practices.

Patterns of daily survival and nesting success

I analyzed each of the nine grassland bird species separately. However, my primary objective was to test whether grassland management practices affect nesting success of grassland bird species. Consequently, I tested whether the general patterns of daily nest success rate of the nine grassland species differed across management regimes. This test was done using a combined probabilities test (Sokal and Rolf 1995) that utilizes a series of separate significance tests on different sets of data that test the same scientific hypothesis. Although the test on the individual species furnishes a probability value that may or may not be statistically significant, the combined probabilities from separate tests of significance may reveal a generalized pattern that would not be statistically detected by separate analyses (Sokal and Rolf 1995).

Cause-specific nest mortality

To determine the mechanisms that limit reproductive success among management regimes, I divided the total daily nest mortality into cause-specific components. To do this, I

summed the total number of nest failures due to each cause-specific component (source of mortality) and divided that number by the total number of observation days. Daily cause-specific nest mortality was calculated for each species and by year. For each species, I tested whether cause-specific daily nest mortality differed among treatment using a Chi-Square analysis with multiple comparisons (Hines and Saucer 1989). I used a combined probabilities test (Sokal and Rolf 1995) to determine whether the general patterns of daily cause-specific nest mortality differed across management regimes.

I performed all the statistical analyses using STATISTICA software (StatSoft Inc, 2000) unless stated otherwise. Significance levels for statistical tests were set at $P < 0.05$. Percentage data were arc-sine transformed.

RESULTS

Effects of management regimes on vegetation

Vegetation characteristics varied significantly between management regimes (Table 1). Pairwise comparisons of all vegetation variables showed more ground vegetation cover, higher vegetation structure (foliage density and cover), and greater heterogeneity under light than heavy grazing pressure (Table 1, $P < 0.001$ for all pairwise comparisons). Similarly, pairwise comparisons of all vegetation variables examined showed that vegetation differed between burning regimes with annual burning having the lowest values (Table 1, $P < 0.001$ for all pairwise comparison). Logistic regression indicated a significant overall difference in vegetation structure between heavily grazed and lightly grazed (likelihood ratio $\chi^2 = 46.85$, $P < 0.0001$), and between annually burned and biennially burned treatments (likelihood ratio $\chi^2 = 35.47$, $P < 0.001$). Stepwise discriminant function analysis (SDFA) selected two vegetation variables as the main variables that separated between grazing regimes (Wilks' lambda = 0.274, $F = 43.66$, df = 2, 33, $P < 0.0001$). These two variables, in short, depicted aspects of structural vegetation (MAXHGT) and vertical heterogeneity (VFD10). Similarly, SDFA selected 6 main vegetation variables that differentiated between burning regimes (Wilks' lambda = 0.268, $F = 13.20$, df = 6, 29, $P < 0.0001$) – one cover variable (%TOTGVCOV), three structural vegetation variables (MAXHGT, HIT0-10, and TOTHITS) and two horizontal heterogeneity variables (HFD10 and CVMAXHGT). SDFA on all the three management regimes yielded two highly significant canonical axes ($\chi^2 > 23.67$, $P < 0.001$ in both cases) that strongly differentiated vegetation between management regimes (Mahalanobis – $P < 0.001$, $F > 11.05$, df = 7, 45

for all pairwise comparisons). Predictor variables selected by this SDFA were a cover variable (%HCOV), two structural vegetation variables (MAXHGT and HIT0-10) and four heterogeneity variables (HFD10, CVMAXHGT, CVTOTHITS and VFD10).

Effects of grazing pressure on nest success

For breeding purposes, all the study species apart from GP, RCL and RL avoided the heavily grazed treatment. Daily nest success rate of GP differed significantly between grazing treatments (Table 2a). RCL and RL showed a similar trend, but sample sizes were too low to show statistical significance (Table 2a). Overall daily nest survival and daily nest survival during egg stage for GP were significantly higher (Chi-Square; $\chi^2 > 5.28$, df = 1, $P < 0.05$ in both cases) under light than heavy grazing. However, there was no difference between treatments in daily nest survival during the nestling stage ($P > 0.05$). Results of combined probabilities from independent tests for each species indicated that the general pattern of daily success rates of nests was affected by grazing (Table 2a). Overall daily nest survival and daily nest survival during nestling stage were greater under biennial than under annual burning ($\chi^2 > 12.92$, df = 6, $P < 0.05$ in both cases). Daily nest survival during the egg stage did not differ between treatments ($P > 0.05$).

Table 1. The means of vegetation characteristics between (1) H+A versus L+A grasslands, and (2) L+A versus L+B grasslands (H+A = heavy grazing with annual burning, L+A = light grazing with annual burning, L+B = light grazing with biennial burning) in the Wakkerstroom high-altitude grasslands. "Data were analysed using Wicoxon pairwise comparisisons and univariate ANOVA." Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

Vegetation variables	Effects of grazing					Effects of burning				
	Mean value (±SD)		ANOVA		Wilcoxon	Mean value (±SD)		ANOVA		Wilcoxon
	H+A	L+A	F	*P*	*P*	L+A	L+B	F	*P*	*P*
Coverage										
% TGCOV	94.0 (11.0)	98.0 (8.0)	19.4	0.001	***	98.0 (8.0)	99.0 (20.0)	5.2	0.029	***
% GCOV	81.0 (10.0)	88.0 (10.0)	19.0	0.001	***	88.0 (10.0)	91.0 (20.0)	8.1	0.007	***
% HCOV	13.0 (4.0)	10.0 (4.0)	6.2	0.018	***	10.0 (4.0)	8.0 (1.0)	6.0	0.019	***
Horizontal structure										
Hit0-10	1.52 (0.99)	3.58 (0.94)	40.6	0.001	***	3.58 (0.94)	5.46 (0.95)	36.0	0.001	***
Vertical structure										
MAXHGT	8.11 (3.33)	18.50 (5.52)	46.7	0.001	***	18.50 (5.52)	27.69(6.09)	22.5	0.001	***
TOTHITS	1.63 (1.09)	4.18 (1.33)	39.4	0.001	***	4.18 (1.33)	11.10(6.13)	21.9	0.001	***
Horizontal Heterogeneity										
HFD10	2.23 (0.67)	1.31 (0.42)	25.0	0.001	***	1.31 (0.42)	2.65 (2.48)	5.1	0.030	***
CVMAXHGT	0.67 (0.09)	0.56 (0.08)	12.4	0.001	***	0.56 (0.08)	0.49 (0.09)	7.0	0.012	***
CVTOTHITS	1.11 (0.29)	0.70 (0.19)	26.0	0.001	***	0.70 (0.19)	0.66 (0.25)	0.3	0.602	***
Vertical Heterogeneity										
VFD10	0.63 (0.26)	0.71 (0.59)	0.22	0.645	***	0.71 (0.59)	2.66 (1.90)	17.4	0.001	***

Table 2a. Daily survival probability (± SE) of nests for each species, as calculated according to Mayfield (1975), on heavily grazed (H+A) and lightly grazed grasslands (L+A).

Species	Stage	Number of nests (n_1; n_2)[b]	Total days exposure (E_1; E_2)[c]	Daily survival probability (SE)[a]		χ^2	df	*P*
				H+A	L+A			
Grassveld Pipit	Overall	42; 214	421; 2660.5	0.924 (0.0129)	0.958 (0.0039)	6.36	1	0.0116
	Eggs	37; 168	245; 1349.5	0.918 (0.0175)	0.960 (0.0053)	5.28	1	0.0216
	Nestling	22; 156	175.5; 1311	0.932 (0.0191)	0.956 (0.0057)	1.45	1	0.2286
Red-capped Lark	Overall	2; 6	8.5; 56.5	0.764 (0.1455)	0.947 (0.0298)	1.52	1	.02179
	Eggs	2; 4	8.5; 21.5	0.764 (0.1455)	0.861 (0.0747)	0.35	1	0.5531
	Nestling	0; 3	0; 35	0.000 (0.0000)	1.000 (0.0000)			0.0001
Rudd's Lark	Overall	1; 11	6.5; 97	0.846 (0.1415)	0.918 (0.0279)	0.25	1	0.6176
	Eggs	1; 11	6.5; 64	0.846 (0.1415)	0.938 (0.0303)	0.40	1	0.5249
	Nestling	0; 6	0; 33	0.000 (0.0000)	0.879 (0.0568)			0.0001
Combined probability	Overall				*$-2\sum lnP$, df, (P)*	12.92	6	0.0500
	Eggs				*$-2\sum lnP$, df, (P)*	10.14	6	0.5500
	Nestling				*$-2\sum lnP$, df, (P)*	39.79	6	0.0010

[a] SE as calculated under the method of Johnson (1979).
[b] n_1 = number of nests on H+A; n_2 = number of nests on L+A.
[c] E_1 = total exposure days in H+A; E_2 = total exposure days in L+A.

Effects of burning frequency on nesting success

Daily nest success rates were similar among years (Appendix 1). Consequently, all these data were pooled for subsequent analysis. I analyzed each of the nine grassland species separately (see Table 2b). Independent analysis of each species showed that daily nest survival for GP were similar between management treatments (Table 2b), while daily nest survival for YBP, OTL, AC, and LTW were higher in the biennially burned than in annually burned plots (Table 2b). QF, CQ, and RCL showed similar trends, but their sample size were too low to show statistical significance. RL did not breed under biennial burning treatment. Results of combined probabilities from independent tests for each species indicated that the general pattern of daily success rates of nests was affected by burning treatment (Table 2b). Overall, daily nest survival throughout the breeding period, daily nest survival during the incubation stage, and daily nest survival during the nestling stage were all greater under biennial burning than under annual burning (χ^2 >39.74, df = 16 (14 for nestling stage), $P < 0.0001$ in all cases).

Causes of nest failure

The main cause of nest mortality was nest predation irrespective of grazing pressure (Table 3), and accounted for > 87 % of total nest failures. Similarly, the major cause of nest mortality was nest predation irrespective of burning frequency (Table 3), and accounting for > 70 % of total nest failures. Daily nest mortality as a result of nest predation differed between grazing (χ^2 =12.90, df = 6, $P < 0.05$) and burning treatments (χ^2 = 59.34, df = 16, $P < 0.001$). Failure due to other mortality cause factors were insignificant and did not differ between management regimes (P > 0.05 in all cases).

Experimental nests

Daily nest success rates for artificial clutches were affected by burning frequency between treatments (Table 4). Using Mayfield estimates of daily survival rates, daily nest survival for artificial clutches were significantly higher under biennial burning than under annual burning (χ^2 = 9.92, df = 1, P < 0.002).

Table 2b. Daily survival probability (± SE) of nests for each species, as calculated according to Mayfield (1975), on annually burned grassland (L+A) and biennially burned grasslands (L+B).

Species	Stage	Number of nests (n_2; n_3) [b]	Total days exposure (E_2; E_3)[c]	Daily survival probability (SE)[a] L+A	Daily survival probability (SE)[a] L+B	χ^2	df	*P*
Grassveld Pipit	Overall	214; 94	2660.5; 1331	0.958 (0.0039)	0.965 (0.0051)	1.19	1	0.2756
	Eggs	168; 79	1349.5; 659	0.960 (0.0053)	0.971 (0.0065)	1.72	1	0.1897
	Nestling	156; 74	1311; 672	0.956 (0.0057)	0.958 (0.0077)	0.04	1	0.8346
Yellow-breasted Pipit	Overall	171, 78	1697.5, 1211.5	0.939 (0.0058)	0.980 (0.0040)	33.86	1	0.0001
	Eggs	123; 57	901; 561.5	0.936 (0.0082)	0.972 (0.007)	11.15	1	0.0008
	Nestling	114; 64	796.5; 650	0.944(0.0082)	0.988 (0.0043)	22.58	1	0.0001
Orange-throated Longclaw	Overall	115; 80	1087.5; 1141.5	0.936 (0.0074)	0.978 (0.0043)	24.08	1	0.0001
	Eggs	87; 61	546; 512.5	0.919 (0.0116)	0.969 (0.0077)	12.90	1	0.0003
	Nestling	70; 72	540; 629	0.952 (0.0092)	0.986 (0.0047)	10.83	1	0.0010
Ayre's Cisticola	Overall	123; 35	1685.5; 537	0.961 (0.0047)	0.980 (0.0061)	6.09	1	0.0136
	Eggs	96; 26	812; 203.5	0.948 (0.0078)	0.980 (0.0109)	5.70	1	0.0170
	Nestling	78; 30	871; 333.5	0.972 (0.0055)	0.982 (0.0073)	1.20	1	0.2739
Long-tailed Widow	Overall	67; 69	863; 1189.5	0.951 (0.0073)	0.970 (0.0050)	4.61	1	0.0318
	Egg	52; 58	455; 651.5	0.945 (0.0107)	0.977 (0.0063)	6.64	1	0.0100
	Nestling	42; 56	408; 628	0.958 (0.0099)	0.963 (0.0075)	0.16	1	0.6873
Quail Finch	Overall	9; 27	133; 415	0.947 (0.0129)	0.971 (0.0082)	2.47	1	0.1164
	Egg	9; 25	79; 209	0.949 (0.0247)	0.952 (0.0148)	0.01	1	0.9170
	Nestling	5; 17	54; 206	0.944 (0.0312)	0.990 (0.0068)	2.08	1	0.1497
Rudd's Lark	Overall	11; 0	97; 0	0.918 (0.0279)				
	Egg	11; 0	64; 0	0.938 (0.0303)				
	Nestling	6; 0	33; 0	0.879 (0.0568)				
Red-capped Lark	Overall	6; 2	56.5; 26	0.947 (0.0298)	1.000 (0.0000)	3.16	1	0.0753
	Egg	4; 1	21.5; 3	0.861 (0.0747)	1.000 (0.0000)	3.46	1	0.0628
	Nestling	3; 2	35; 23	1.000 (0.0000)	1.000 (0.0000)			1.0000
Common Quail	Egg	25,5	197.5;	0.936 (0.01756)	0.966 (0.0236)	1.04	1	0.3082
Combined probability	Overall				**$-2\sum\ln P$, df, (P)**	66.74	16	0.0001
	Egg				**$-2\sum\ln P$, df, (P)**	59.23	16	0.0001
	Nestling				**$-2\sum\ln P$, df, (P)**	39.74	14	0.0001

[a] SE as calculated under the method of Johnson (1979).
[b] n_1 = number of nests on H+A; n_2 = number of nests on L+A; n_3= number of nests on L+B.
[c] E_2 = total exposure days in L+A; E_3= total exposure days in L+B.

Table 3. Daily mortality of study species among the three management treatments (H+A, L+A, and L+B) partitioned by cause of nest failure.

Species	Treatment[a]	Daily mortality failed by any cause	Daily mortality partitioned into cause of nest failure				
			Predation	Trampling	Desertion	Weather	Adult mortality and starvation
Grassveld Pipit	H+A	0.078	0.071	0.002	0.002	0.002	0.000
	L+A	0.044	0.038	0.002	0.003	0.001	0.000
	L+B	0.035	0.032	0.001	0.002	0.001	0.001
χ^2, df, (P)	Grazing	6.17, 1, (0.013)	6.37, 1, (0.012)	0.00, 1, (1.000)	0.15, 1, (0.703)	0.17, 1, (0.681)	
	Burning	1.96, 1, (0.161)	0.98, 1, (0.322)	0.89, 1, (0.346)	0.34, 1, (0.562)	0.00, 1, (1.000)	1.45, 1, (0.228)
Red-capped Lark	H+A	0.235	0.235	0.000	0.000	0.000	0.000
	L+A	0.053	0.053	0.000	0.000	0.000	0.000
	L+B	0.000	0.000	0.000	0.000	0.000	0.000
χ^2, df, (P)	Grazing	1.50, 1, (0.220)	1.50, 1, (0.220)				
	Burning	3.16, 1 (0.076)	3.16, 1 (0.076)				
Rudd's Lark	H+A	0.154	0.154	0.000	0.000	0.000	0.000
	L+A	0.082	0.082	0.000	0.000	0.000	0.000
χ^2, df, (P)	Grazing	0.25, 1 (0.618)	0.25, 1 (0.618)				
Yellow-breasted Pipit	L+A	0.061	0.054	0.002	0.002	0.001	0.001
	L+B	0.020	0.018	0.001	0.001	0.000	0.000
χ^2, df, (P)	Burning	33.94, 1 (0.001)	28.80, 1, (0.001)	0.48, 1, (0.488)	0.48, 1, (0.488)	1.45, 1, (0.228)	2.87, 1, (0.090)
Orange-throated Longclaw	L+A	0.064	0.060	0.003	0.001	0.000	0.001
	L+B	0.022	0.020	0.001	0.001	0.000	0.000
χ^2, df, (P)	Burning	23.80, 1 (0.001)	23.19, 1, (0.001)	1.21, 1, (0.271)	0.00, 1, (1.000)		1.18, 1, (0.277)
Ayre's Cisticola	L+A	0.039	0.027	0.009	0.002	0.001	0.000
	L+B	0.020	0.015	0.004	0.002	0.002	0.000
χ^2, df, (P)	Burning	6.06, 1, (0.014)	3.40, 1, (0.065)	2.06, 1, (0.1516)	0.00, 1, (1.000)	0.24, 1, (0.624)	
Long-tailed Widow	L+A	0.050	0.038	0.002	0.003	0.000	0.006
	L+B	0.030	0.024	0.002	0.002	0.000	0.003
χ^2, df, (P)	Burning	5.02, 1, (0.025)	3.13, 1, (0.077)	0.00, 1, (1.000)	0.18, 1, (0.667)		1.03, 1, (0.311)
Quail Finch	L+A	0.053	0.053	0.000	0.000	0.000	0.000
	L+B	0.029	0.029	0.000	0.000	0.000	0.000
χ^2, df, (P)	Burning	1.30, 1, (0.254)	1.30, 1, (0.254)				
Common Quail	L+A	0.063	0.063	0.000	0.000	0.000	0.000
		0.033	0.033	0.000	0.000	0.000	0.000
χ^2, df, (P)	Burning	0.65, 1, (0.420)	0.65, 1, (0.418)				
Combined probability	**-2∑lnP, df, (P) - Grazing**	12.67, 6, (0.05)	12.90, 6, (0.05)	0.00, 2, (1.00)	0.70, 2, (0.70)	0.77, 2, (0.70)	-
	-2∑lnP, df, (P) - Burning	66.06, 16, (0.001)	59.34, 16, (0.001)	9.94, 10, (0.40)	3.40, 10, (0.97)	3.90, 6, (0.70)	12.67, 8, (0.20)

[a]H+A = Heavily grazed and annually burned; L+A = Lightly grazed and annually burned; L+B = Lightly grazed and biennially burned.

Table 4. Comparison of daily probability of success of artificial clutches placed in natural nests belonging to three major ecologically similar species calculated using Mayfield (1961,1975) on annually burned (L+A) and biennially burned grassland (L+B).

Species	L+A	L+B	χ^2	df	P
All	0.961 (0.00484)	0.980 (0.00360)	9.9	1	0.002
Grassveld Pipit	0.955 (0.00850)	0.974 (0.00684)	3.0	1	0.082
Yellow-breasted Pipit	0.967 (0.00677)	0.981 (0.00608)	2.4	1	0.124
Orange-throated Longclaw	0.957 (0.01121)	0.988 (0.00523)	6.3	1	0.012

Effects of season on vegetation across management regimes

Vegetation characteristics (foliage density, height, cover and heterogeneity) increased significantly through the season in H+A treatment (ANOVA, $P < 0.007$), in L+A treatment (ANOVA, $P < 0.001$) but not in L+B treatment ($P > 0.05$).

Seasonal patterns in daily nesting success

Independent analysis of daily nest success probabilities across seasons showed a mixed response for each species (Table 5). Results of combined probabilities from independent tests for each species, however, indicated that the general pattern of daily success rates of nests was affected by season (Table 5). Daily nest success differed significantly at different times of the season on both annually burned ($\chi^2 = 40.58$, df = 16, $P < 0.001$) and on biennially burned plots ($\chi^2 = 42.57$, df = 14, $P < 0.001$). Patterns of daily nest success were significantly higher later in the season on both annually burned ($\chi^2 = 45.61$, df = 16, $P < 0.001$) and biennially burned plots ($\chi^2 = 36.81$, df = 14, $P < 0.005$). There was no difference in patterns of daily nest success between the mid-season and early-season on either burning treatment ($P > 0.05$ in both cases).

Table 5. Daily probability survival of nests for each species at different times of the season on annually burned treatment (L+A) and biennially burned grassland (L+B).

L+A

	SPECIES									
SEASON	**GP**	**YBP**	**OTL**	**AC**	**LTW**	**CQ**	**QF**	**RL**	**RCL**	**Combined probability**
OCT-NOV (1)	0.963	0.931	0.943	0.933	0.857			0.750	0.947	
DEC-JAN (2)	0.950	0.888	0.907	0.962	0.946	0.976	0.962	0.908		
FEB-APR (3)	0.967	0.939	0.961	0.955	0.950	0.936	0.938	0.964		*-2∑lnP, df, (P)*
χ^2 (1&2), df, (P)	1.76, 1, (0.1848)	4.06, 1, (0.0438)	2.14, 1, (0.1435)	2.05, 1, (0.1524)	0.45, 1 (0.5021)			1.37, 1, (0.2416)		21.50, 14, (0.100)
χ^2 (2&3), df, (P)	3.39, 1, (0.0657)	12.90, 1, (0.0003)	12.02, 1, (0.0005)	0.34, 1, (0.5583)	0.06, 1, (0.8038)	1.91, 1, (0.1667)	0.40, 1, (0.5251)	0.98, 1, (0.3225)		45.61, 16, (0.001)
χ^2 (1, 2, &3), df, (P)	3.93, 2, (0.1400)	13.38, 2, (0.0012)	12.03, 2, (0.0024)	2.20, 2, (0.3325)	0.53, 2, (0.7684)	1.91, 1, (0.1667)	0.40, 1, (0.5251)	3.54, 2, (0.1707)		40.58, 16, (0.001)

L+B

	SPECIES									
SEASON	**GP**	**YBP**	**OTL**	**AC**	**LTW**	**CQ**	**QF**	**RL**	**RCL**	**Combined probability**
OCT-NOV (1)	0.969	0.963	0.964	0.990	0.964	0.959			1.000	
DEC-JAN (2)	0.952	0.972	0.981	0.974	0.970	0.971	0.953			
FEB-APR (3)	0.765	0.997	0.985	0.981	0.986	1.000	0.976			*-2∑lnP, df, (P)*
χ^2 (1&2), df, (P)	2.29, 1, (0.1302)	0.53, 1, (0.4685)	1.85, 1, (0.1735)	1.50, 1, (0.2201)	0.05, 1, (0.8158)	0.07, 1, (0.7881)				13.01, 12, (0.700)
χ^2 (2&3), df, (P)	1.65, 1, (0.1996)	10.45, 1, (0.0012)	0.22, 1, (0.6424)	0.11, 1, (0.7349)	9.30, 1, (0.0023)	2.12, 1, (0.1452)	1.22, 1, (0.2691)			36.81, 14, (0.005)
χ^2 (1, 2, &3), df, (P)	4.16, 2, (0.1248)	19.38, 2, (0.0001)	2.67, 2, (0.2629)	1.51, 2, (0.4710)	10.02, 2, (0.0067)	3.17, 2, (0.2046)	1.22, 1, (0.2691)			42.6, 14, (0.001)

DISCUSSION

My results on the effects of management-induced disturbance on vegetation are in accordance with other studies (e.g. see Milchnas *et al.* 1988, Bullock & Pakeman 1997, Van der Koppel *et al.* 1997, Dupré and Diekmann 2001). My study demonstrates a clear relationship between nesting success and both burning and grazing practices. My results are in general agreement with published studies that show strong effects of management practices on bird populations (e.g. see Saab 1995, Ammon and Stacey 1997).

Effects of fire and grazing management practices on nesting vegetation and nesting success

Fire can affect ecosystems negatively or positively depending on variation of its use and application (also see Bullock and Pakeman 1997). Farmers in the Wakkerstroom study area burn immediately after the onset of summer rains and use it to control ticks and disease, improve forage for grazing – sour to sweet grass, manage competing vegetation, remove accumulated litter, and regenerate new grass. Although the optimal burning frequency is supposed to vary according to the rate of litter accumulation (Stuart-Hill and Mentis 1982), most farmers in South African high altitude grasslands burn their farms annually, or more frequently, irrespective of litter accumulation (Tainton1981). Domestic livestock does not simulate a natural ecological result as wild herbivores used to do (e.g. see McNaughton 1986). The shift from wild to domestic grazing has thus changed the nature of grazing and intensified the effect of grazing on grassland habitats and their fauna. In my study area, timing of grazing is not dependent on sward height as it should (Mentis 1981, Tainton 1981), but on the time when poisonous Grass Tulips die off; i.e. normally three weeks to a month after the burn (personal communication with farmers). Cattle are thus introduced into grazing paddock before the grass height reaches the recommended sward height of 25cm (Mentis 1981, Tainton 1981). The combined effect of frequent fires and overgrazing leads to the removal or reduction of nesting vegetation cover, reducing nest concealment and making nests more visible to nest predators (Also see Wiens 1969, Jackson et al. 1988, Martin and Roper 1988, Martin 1988c, Knopf 1995, Ammon and Stacey 1997, Chapter 5). Consistent differences in predation rates due to variation in management-mediated habitat quality can favour contrasting life-history traits (e.g. see Lack 1968, Martin 1993a), and merits further investigation.

Seasonal pattern in nesting success

As expected, vegetation characteristic (foliage density, height, cover and heterogeneity) increased through the season. My results show that livestock grazing and fire affect vegetation characteristics (vegetation cover, density and heterogeneity) of the breeding habitat, which in turn influences nesting mortality probabilities. Further, nest mortality decreased with an increase in plot vegetation cover and density, which provided greater concealment for nests. Growth in vegetation during the season may provide greater concealment with time, thereby reducing visibility of nests during late season, which enhances nest survival. This demonstrates that habitat structure, as altered by fire frequency and grazing intensity, is indeed the causal agent of the observed trend in nesting success.

Underlying mechanism linking grassland bird population declines to management practices

This study provides support for the hypothesis that potential demographic consequences of grazing and burning effects include altered susceptibility to reproductive failure (Ammon and Stacey 1997). Partitioning causes of nest mortality into cause-specific components has important consequences for understanding the mechanisms that limit avian reproductive success. Daily mortality as a result of nest predation accounted for the majority of nest failures under all management regimes for all species. This result suggests that livestock grazing and fire may not only affect abundance and availability of nesting vegetation, but could influence bird populations by facilitating nest predation. This further emphasizes the primary role of nest predation as a selective force. Direct impacts of grazing and fire through removal of cover of active nests, disturbance of nests, or direct mortality through trampling and burning of nests apparently are of little consequence. Grazing and burning rarely harm birds directly. Instead, the negative impact of grazing and burning could be indirectly linked to increased nest predation.

These findings concerning nesting success and the mechanisms limiting nesting success (nest predation) suggest a possible link between fire frequency and grazing intensity on the one hand, and declines in bird populations. Although I was able to explicitly demonstrate that management-mediated nest predation could be the cause of population declines, other possible alternatives needs to be considered as well. Single causal explanations may not be sufficient while developing strategies to mitigate and/or curb the current trends in avian population declines. Management practice-mediated

reproductive dysfunction via nest predation could be a more important factor than even food availability in regulating populations of the birds that live in South Africa's highland grassland ecosystems. Nest predation has similarly been linked to population declines of for example, Neotropical migratory birds (see Wilcove 1985, Donovan *et al.* 1995, Ammon and Stacey 1997). Because nesting success for all eight focal species in this study were affected similarly by grazing and burning regimes, this pattern might hold for many other grassland nesting birds.

Persistent renesting attempts after nesting failure and multiple brooding effort by successful pairs can offset high nest mortality rates to some extent (Martin 1992). Such compensation may not be possible in heavily disturbed grassland systems where predation is common throughout the breeding season. The low nest success that I observed in my study could well be below the level needed to balance expected mortality and could thus affect population size and cause the ultimate loss of some grassland species. Indeed, nesting success rates below 30% (whole cycle) have been implicated in population declines in Neotropical migrants (Donovan *et al.* 1995) and shrubsteppe songbirds (Yanes and Suárez 1995).

Appendix 1. Daily probability (SE) of survival of nests, calculated according to Mayfield (1961,1975) on annually and biennially burned grassland plots for all nests in each breeding season.

Species	Treatment	Year	Number of nests (N, n)	Total days exposure	Daily survival probability[a]	χ^2	df	P
Grassveld Pipit	L+A	1998-1999	53 (26)	727.5	0.964 (0.00688)			
		1999-2000	61 (27)	835	0.968 (0.00612)			
		2000-2001	100 (51)	1098	0.954 (0.00635)	2.63	2	0.2681
	L+B	1998-1999	8					
		1999-2000	59 (30)	898	0.967 (0.00600)			
		2000-2001	27 (11)	369	0.970 (0.00885)	0.078	1	0.7790
Yellow-breasted Pipit	L+A	1998-1999	31 (21)	341.5	0.939 (0.01300)			
		1999-2000	64 (36)	635.5	0.943 (0.00917)			
		2000-2001	75 (45)	707.5	0.936 (0.00917)	0.26	3	0.8639
	L+B	1998-1999	4					
		1999-2000	45 (14)	774.5	0.982 (0.00479)			
		2000-2001	29 (7)	380	0.982 (0.00690)	0.00	1	1.000
Orange-throated Longclaw	L+A	1998-1999	36 (25)	370.5	0.933 (0.01303)			
		1999-2000	34 (20)	298	0.933 (0.01449)			
		2000-2001	45 (25)	419	0.940 (0.01157)	0.22	2	0.8980
	L+B	1998-1999	4					
		1999-2000	38 (12)	586.5	0.980 (0.00585)			
		2000-2001	38 (12)	529	0.977 (0.00647)	0.12	1	0.7309
Ayre's Cisticola	L+A	1998-1999			0.959 (0.00534)			
		1999-2000	35 (19)	507.5	0.963 (0.00843)			
		2000-2001	41 (25)	518	0.952 (0.00942)	0.77	2	0.6808
	L+B	1998-1999	3					
		1999-2000	23	343	0.980			
		2000-2001	9					
Long-tailed Window	L+A	1998-1999	22 (13)	290	0.955 (0.01215)			
		1999-2000	26 (19)	360	0.947 (0.01178)			
		2000-2001	19 (10)	213	0.953 (0.01449)	0.24	2	0.8871
	L+B	1998-1999	7					
		1999-2000	46 (25)	809.5	0.970 (0.00608)			
		2000-2001	16 (7)	271	0.974 (0.00964)	0.12	1	0.7256

[a] SE as calculated under the method of Johnson 1979.

3

Effects of grassland management practices on density, clutch initiation, clutch size and duration of breeding

Abstract.

Grassland management practices may have profound effects on grassland birds' natural history and life history. I used a comparative approach to examine the effect of management practices on the distribution, abundance, clutch size and clutch initiation of grassland birds. The study was conducted in the high altitude grasslands at Wakkerstroom, South Africa, from 1998 through 2001. Study plots were set out in heavily grazed and annually burned grasslands (H+A), lightly grazed and annually burned grasslands (L+A), and lightly grazed and biennially burned grasslands (L+B). I measured vegetation characteristics across management regimes, surveyed bird densities and searched for nests to explore their distribution, nest initiation dates, clutch size and duration of breeding under each of the three management regimes. Vegetation density, cover and heterogeneity were lowest in H+A, intermediate in L+A, and highest in L+B grasslands. Thus management practices clearly affected the distribution and abundance of bird species. Although birds occurred at low densities in H+A grasslands, only three out of eight focal species bred there at all. Pairs with territories located in biennially burned grassland started nesting earlier than their counterparts in annually burned grasslands, thus effectively shortening the breeding season in the latter. Grazing and burning only affected the clutch size of Grassveld Pipits and Long-tailed Widows respectively. This difference in clutch size was caused by management-mediated nest predation rather than food abundance. I propose that intensive grazing pressure and periodic burning should be relaxed by reducing stocking rates and burning less frequently to benefit grassland bird species.

Key words: Grassland bird abundance, nest density, egg initiation, clutch size, duration of breeding, livestock grazing, burning.

INTRODUCTION

Although the general trend in variation of life-history strategies among species has been attributed to trade-offs maximising lifetime reproductive output (Roff 1992), life histories could be influenced by historical, physical, environmental, and phylogenetic constrains

(Stearns 1992). For example, offspring production (e.g. timing of breeding, clutch size and duration of breeding) may be constrained by temperature, season, and by life history trade-offs that may be caused by food limitation (Lack 1947) or predation (Lima 1987, Stearns 1992, Martin and Clobert 1996). The causes and causal mechanisms producing variation in avian life histories and the hypotheses explaining these differences are poorly understood. Although a variety of traits can be influenced by costs associated with local conditions, one trait that seems consistently modified is clutch size (Skutch 1949, Lima 1987, Martin 1988). Despite the fact that clutch size is one of the traits showing close adjustments to local conditions (Lack 1968), the proximate mechanism by which clutch size is adjusted remains uncertain in the many cases.

Grassland management regimes can change the diversity, dominance, cover and structure of grassland plant communities (e.g. see Milchnas *et al.* 1988, Bullock and Pakeman, 1997, Van der Koppel *et al.* 1997, Dupré and Diekmann 2001, Chapter 2). The defoliation of grassland by disturbance regimes (herbivory and fire) can potentially have positive or negative consequences for the various members of the food chain that live there (e.g. see Dickson 1981, Curry 1994). Reduced availability of food, for example, is predicted to affect bird densities (e.g. see Milchnas *et al.* 1988), limit clutch size (Ruiz *et al.* 2000) and number of breeding attempts (Martin 1987, 1992, Rodenhouse 1986), and will therefore to influence breeding productivity. Destruction and alteration of breeding habitat could also affect abundance and behaviour of predators (Martin 1993b). Individuals can respond to high nest predation pressure in a variety of ways. They can reduce their investment at any one breeding attempt by reducing clutch size (Skutch 1949, Martin *et al.* 2000a, Murphy 2000, Bosque and Bosque 1995), increase the number of breeding attempts (Martin 1992) or avoid areas of high predation risk altogether (e.g. see Blancher and Robertson 1985).

Livestock farming is one of the primary land uses of privately-owned grasslands in South Africa. Both periodic fire and grazing have historically been prominent features of the natural ecology of the grasslands and both continue to be important ecological processes today (e.g. see Wade and Lundsford 1990). In South Africa, the role of fire and grazing in maintaining grassland systems is well known in as far as it affects livestock production, but little is known of their effects on grassland birds (Mentis 1981, Macdonald 1989, O'Connor and Bredenkamp 1997).

Given the general poor conservation status of many grassland birds in South Africa (see Tarboton 1997b), it is crucial to understand the mechanisms of how grassland management practices affect bird breeding.

In this chapter, I evaluate the effects of defoliation (by grazing and burning) on grassland birds concerning their abundance, densities and interspecific interactions, (2) nest densities and distribution (3) clutch initiation and duration of the breeding season, and (4) clutch size. To this end, two alternatives are possible: (i) clutch size decrease with increased risk of nest predation, and (ii) clutch size decreases with a decrease in food abundance. The hypothesis here is that if clutch size could be shown to be similar comparing areas with equal food abundance, then any differences would be a result of nest predation and vice versa.

METHODS

Study area

The study was conducted in the high-lying grassland (between 1800m to 2250m elevations) of Wakkerstroom (centred at 27° 10' S, 30° 06' E), South Africa, from 1998-2001. The main vegetation types with respect to altitude and soil type as classified by Low and Rebelo (1996) are Moist Sandy Highveld Grassland dominated by *Themeda triandra*, *Digitaria thicholaenoides*, *Tristachya leucothrix* and *Hetropogon contortus*; North-eastern Mountain Grassland which is dominated by *Tristachya leucothrix, Loudetia simplex and Diheteropogon filifolius*; Moist Clay Highveld Grassland dominated by *Themeda triandra* and Natal Central Bushveld. The main land use in the Wakkerstroom district is large-scale livestock farming, mainly beef cattle. The district experiences mild to warm summers, and cold and dry winters with occasional snow. Rain falls in summer at an average rate of between 700 mm and 1200 mm. The highland grassland of Mpumalanga has been under considerable grazing pressure since the 1930s (Downing 1978, Edwards 1981, Hockey *et al.* 1988). Also, although the optimal burning frequency is supposed to vary according to the rate of litter accumulation (Stuart-Hill and Mentis 1982), most farmers in Mpumalanga burn their farms annually irrespective of litter accumulation (Tainton1981). As a result, over 90 % of the grassland get burned every year.

Experimental design

I controlled for slope in my selection of and selected plots representing three sets of grassland management systems, viz. heavily grazed and annually burned (H+A), lightly grazed and annually burned (L+A), and lightly grazed and biennially burned (L+B). Six replicate grassland plots were used for each management system. The grassland plots (experimental units) were separated from others by at least 500m wide strips and were all within 10 km^2 of continuous grassland. Study plots were 25 ha in size. Grazing intensity was standardised to large animal units (LAU). One LAU is equivalent to 1 cow (454 kg) or 5 sheep (Booysen 1967, Owen-Smith and Dankwerts 1997). Heavy grazing intensity was assumed to be > 3 LAU/ha and light grazing was < 1.5 LAU/ha.

Censusing

I estimated bird abundance using a modification of the fixed-strip or belt transect method (Kendeigh 1944). Birds were counted along three 500m transects per study plot. The transects ran perpendicular to the plot fence and were located at 100m, 250m and 400m from the edge of the plot fence. To census birds, we held a 50 m rope between two observers and dragged it over the vegetation along the transect. These were the same transects used for vegetation survey (Chapter 2). Collectively, the three transects covered an area of 7.5 ha per study plot. Censusing began after territories were established (i.e. November). Study plots were censused monthly during the breeding season (Nov-Apr). Censusing days were divided into three four-hour observation periods (0600–1000 h, 1000–1400 h, 1400–1800 h). Each plot was censused six times during each breeding season, with census sessions spread over the three observation periods in rotation according to a fixed schedule.

Assessment of relative food abundance

Monthly arthropod abundance was sampled along the same three transects used for bird censusing during the entire breeding seasons (October to April the following year) from 1998 through 2001 using sweep nets. These samples consisted of 600 sweeps per plot (200 at each of the 3 transects) during each monthly food survey.

DATA ANALYSIS

During each census, the results of the three transect surveys from each plot were combined to give the mean density of each species. The values used for statistical analysis were single estimates of the population density of each bird species at each plot (derived from the pooled set of the three transect surveys) in each year for each management system. I used a Mann-Whitney U-test to compare mean bird abundance between management systems (H+A and L+A) and (L+A and L+B). Shannon-Wiener index of species diversity (Zar 1984) was calculated for birds between management systems. Similarities in species composition between management systems were determined using Jaccard's coefficient of similarity (Krebs 1999). The index can have values ranging from 0 (perfect dissimilarity) to 1 (perfect similarity). Species richness was simply the number of bird species observed (Wiens 1989).

Since multiple nesting (re-nesting) can inflate nest densities, nest density was calculated over a 15-day period (shortest time between re-nest). Nest density was calculated as the number of nests found per hectare of each management regime during each of the thirteen 15-days blocks, divided by total area of the management treatment. Differences in nest density between management regimes over the 15-day periods were tested using a paired *t*-test across all the species in order to explore general relationships. Parametric *t*-test were computed after transforming nests density (n) to $n = \sqrt{(n + 0.5)}$ to normalise the data (Zar 1984, Sokal and Rohlf 1995). Statistical analysis of nest density was limited to study species with at least 10 nests in any one management system.

Nests initiation dates were calculated according to Martin *et al.* (1997), and included known exact dates of first egg laying, and back-dating from any reliably estimated period (e.g. known hatching date and fledging dates). Only clutches verified as complete were used to determine clutch size. To control for date of clutch initiation clutches laid early (October) and late breeding season (March onwards) were excluded from the analysis. I evaluated this for eight common birds with >25 nests in at least two of the three management systems. Only three of these eight species ever nested in the third management system, viz. H+A.

RESULTS

Effects of management practices on bird density

When I controlled for burning, overall density (birds/ ha) of 48 study bird species were higher (Mann-Whitney U Test: Z = -2.72, $P < 0.006$) on transects in lightly grazed grassland (0.63 ± 0.98) than heavily grazed grassland (0.35 ± 0.72). When I controlled for grazing, overall density (birds/ ha) of the study birds were similar in transects in annually and biennially burned grassland (0.63 ± 0.98) versus (0.56 ± 1.07) (Mann-Whitney U Test: $P >$ 0.05). Individual species showed a mixed response to management grassland disturbance (Tables 1a and b).

Effects of management practices on species richness

Census survey data indicated higher species richness on L+A (n = 41) than on both H+A (n = 19) and L+B (n = 28) grasslands. When all species were considered (Tables 1a and b), there was a significant decrease in species richness with grazing (Student's $t = 9.41$, $P < 0.0001$) and marginally fewer with increasing burning frequency (Student's $t = 1.94$, $P = 0.0516$). The Shannon-wiener diversity (H') was estimated at 2.55, 3.59 and 3.11 for H+A, L+A and L+B respectively. Species similarity indices between grazing systems showed a Jaccard's coefficient of 0.44, while burning showed a coefficient of 0.49.

Effects of management practices on nest density

A total of over 1202 nests were found over the three breeding seasons (Table 2a). Of these, 1182 nests belonged to only nine focal species found within the study area of (810 ha) during the study period (Table 2a). When I controlled for burning, overall nest density (nests/ha) for the nine main study species were significantly higher in lightly grazed (0.18 ± 0.0.21) than in heavily grazed grassland (0.08 ± 0.0.09) (Combined probability, $\chi^2 = 66.37$, df = 24, $P < 0.001$) (Table 2b). Nest densities for each of the 14-day periods and results of paired *t*-test are shown in Table (2b). Only three of the nine species nested in heavily grazed grassland (Table 2a), and they nested there in low densities (Table 2b). RCL was the only species to benefit from heavy grazing: nest densities of the RCL were significantly lower in lightly grazed (0.01 ± 0.02, n = 6) than in heavily grazed grassland (0.04 ± 0.00, n = 9) (Student t-test: $t = 4.05$, df = 25, $P < 0.001$). Nest densities of the GP were significantly higher in lightly grazed (0.47 ± 0.22, n = 42) than in heavily grazed grassland (0.19 ± 0.06)

(Student t-test: t = -4.03, df = 25, $P < 0.001$). The remaining six species entirely avoided heavily grazed grassland for breeding purposes during the study period (Table 2a).

When I controlled for grazing, overall density (nests/ha) representing the nine key study species were significantly higher in biennially burned (0.24 ± 0.26) than in annually burned (0.18 ± 0.0.21) grassland (Combined probability, $\chi^2 = 36.50$, df = 24, $P = 0.05$). Nest densities for each of the 15-day periods and results of paired t-test are shown in Table (2c). Rudd's Lark never nested in biennially burned grassland. LTW and QF apparently benefited from biennially burned grassland: nest densities of LTW, and QF were higher in biennially burned grassland than in annually burned grassland (Student t-test $t > 2.14$, df = 25, $P < 0.05$ in both cases). Grassland burning had little effect on the nest densities of the other five species (Table 2c, $P > 0.05$ in all cases). Nest densities of five major species over 15 days periods in both fire regimes are shown in figures 1 and 2.

Effects of management practices on clutch initiation

All study species bred between October and March each year. Frequency distribution of clutch-initiation dates showed similar shapes and trends for all species (Fig 3a-f). Pairs with territories located in L+B grasslands generally started nesting earlier relative to their counterparts breeding on recently burned (H+A and L+A) grasslands. The first breeding peak and consecutive peaks of laying periods for L+A and H+A grasslands lagged behind that in L+B grassland by at least a month (Fig 3a-f).

Table 1a. Mean (±SD) relative abundance (birds/Ha) for 48 grassland bird species on transects in heavily grazed (H+A) and lightly grazed grassland (L+A) in the high-altitude grasslands of Wakkerstroom (Mann-Whitney U Test). " Focal species are given in bold text."

Species	Mean (SD)		Z	p
	H+A	L+A		
Yellow-breasted Pipit *Henimacronyx chloris*	**0.14 (0.13)**	**0.65 (0.20)**	**-3.42**	**0.0006**
Orange-throated Longclaw *Macronyx capensis*	**0.67 (0.06)**	**1.80 (0.48)**	**-3.46**	**0.0005**
Long-tailed Widow *Euplectus progne*	**0.16 (0.32)**	**2.42 (1.27)**	**-3.38**	**0.0007**
Ayres Cisticola *Cisticola ayresii*	**0.64 (0.53)**	**1.74 (0.61)**	**-2.96**	**0.0030**
Red-capped Lark *Calandrella cinerea*	**2.07 (0.64)**	**1.18 (0.48)**	**2.52**	**0.0119**
Grassveld Pipit *Anthus cinamomerous*	**2.38 (0.67)**	**3.20 (0.43)**	**-2.60**	**0.00938**
Common Quail *Coturnix coturnix*	-	**1.14 (0.37)**	-	-
Quail Finch *Ortygospiza atricollis*	-	**0.46 (0.53)**	-	-
Buff-streaked chat *Oenanthe bifasciata*	0.01 (0.03)	0.07 (0.11)	-0.64	0.5218
Black Crow *Corvus capensis*	0.03 (0.04)	0.07 (0.11)	0.32	0.7488
Crowned Plover *Vanellus coronatus*	0.07 (0.10)	0.13 (0.14)	0.72	0.4712
Southern Ant-eating Chat *Myrmecocichla formicivora*	0.08 (0.10)	0.04 (0.07)	0.64	0.5218
Southern Bald Ibis *Bostrychia hagedash*	0.13 (0.33)	0.25 (0.41)	-0.48	0.6310
Cape Wagtail *Motacilla capensis*	0.01 (0.03)	0.02 (0.05)	-0.08	0.9362
Plain-backed Pipit *Anthus leucophrys*	0.03 (0.05)	0.03 (0.07)	0.3203	0.7488
Cattle Egret *Bubulcus ibis*	0.12 (0.29)	0.13 (0.33)	-0.08	0.9362
African Rock Pipit *Anthus crenatus*	0.01 (0.03)	0.01 (0.03)	0.00	1.0000
Fiscal Shrike *Lanius collaris*	0.02 (0.05)	0.02 (0.05)	0.00	1.0000
Red-breasted Sparrow Hawk *Accipiter rufiventris*	0.01 (0.02)	0.01 (0.02)	0.00	1.0000
Spike-heeled Lark *Chersomanes albofasciata*	0.06 (0.09)	0.06 (0.09)	0.00	1.0000
Black-winged Plover *Vanellus melanopterus*	0.01 (0.03)	-	-	-
Black Harrier *Circus maurus*	-	0.002 (0.005)	-	-
Red-winged Francolin *Francolinus levaillantii*	-	0.02 (0.05)	-	-
Swainsons Francolin *Francolinus swainsoni*	-	0.03 (0.07)	-	-
Blue crane *Anthropoides paradiseus*	-	0.01 (0.03)	-	-
Stanley Bustard *Neotis denhami*	-	0.03 (0.04)	-	-
Blue Korhaan *Eupodotis caerulescens*	-	0.07 (0.07)	-	-
Rudd's Lark *Heteromirafra ruddi*	-	0.18 (0.20)	-	-
Eastern Long-billed Lark *Certhilauda curvirostris*	-	0.16 (0.12)	-	-
Pink-billed Lark *Spizocorys conirostris*	-	0.03 (0.06)	-	-
Sentinel Rock Thrush *Monticola explorator*	-	0.03 (0.04)	-	-
Mountain Chat *Oenanthe monticola*	-	0.04 (0.00)	-	-
Stone Chat *Saxicola torquata*	-	0.02 (0.05)	-	-
Fantailed Cisticola *Cisticola juncidis*	-	0.09 (0.10)	-	-
Cloud Cisticola *Cisticola textrix*	-	0.01 (0.03)	-	-
Pale-crowned Cisticola *Cisticola brunnescens*	-	0.01 (0.03)	-	-
Levaillant's Cisticola *Cisticola tinniens*	-	0.01 (0.03)	-	-
Long-billed Pipit *Anthus similis*	-	0.07 (0.07)	-	-
Buffy Pipit *Anthus vaalensis*	-	0.01 (0.03)	-	-
Cuckoo Finch *Anomalospiza imberbis*	-	0.02 (0.05)	-	-
Cape Canary *Serinus canicollis*	-	0.60 (0.22)	-	-
All	0.35 (0.72)	0.63 (0.98)	-2.72	0.006

Table 1b. Mean (±SD) relative abundance (birds/Ha) for 48 grassland bird species on transects in annually burned (L+A) and biennially burned grassland (L+B) in the high-altitude grasslands of Wakkerstroom (Mann-Whitney U Test). " Focal species are given in bold text."

Species	Mean (SD)		Z	P
	L+A	L+B		
Grassveld Pipit	**3.20 (0.43)**	**1.52 (0.43)**	**3.97**	**0.0000**
Common Quail	**1.14 (0.37)**	**0.03 (0.05)**	**3.97**	**0.0000**
Red-capped Lark	**1.18 (0.48)**	**0.20 (0.09)**	**3.97**	**.00000**
Quail Finch	**0.46 (0.53)**	**1.33 (0.21)**	**-2.90**	**0.00034**
Ayres Cisticola	**1.74 (0.61)**	**1.31 (0.24)**	**2.33**	**0.0198**
Yellow-breasted Pipit	**0.65 (0.20)**	**0.81 (0.22)**	**-1.48**	**0.1388**
Long-tailed Widow	**2.42 (1.27)**	**3.34 (1.52)**	**1.51**	**0.1306**
Orange-throated Longclaw	**1.80 (0.48)**	**1.84 (0.24)**	**-0.76**	**0.4497**
Rudd's Lark	**0.18 (0.20)**	-		
Red-winged Francolin	0.02 (0.05)	0.10 (0.06)	-1.92	0.0547
Blue Korhaan	0.07 (0.07)	0.01 (0.03)	1.20	0.2298
Cape Canary	0.60 (0.22)	0.48 (0.09)	0.72	0.4712
Bald Ibis	0.25 (0.41)	0.04 (0.10)	0.64	0.5218
Stanley Bustard	0.03 (0.04)	0.01 (0.03)	0.48	0.6310
Fiscal Shrike	0.02 (0.05)	0.01 (0.03)	0.08	0.9362
Stone Chat	0.02 (0.05)	0.03 (0.04)	-0.32	0.7488
Fantail Cisticola	0.09 (0.10)	0.11 (0.17)	0.08	0.9362
Cattle Egret	0.13 (0.33)	0.15 (0.28)	-0.32	0.7488
Red-breasted Sparrow Hawk	0.01 (0.02)	0.01 (0.02)	0.00	1.0000
Black Harrier	0.002 (0.005)	0.002 (0.005)	0.00	1.0000
Swainsons Francolin	0.03 (0.07)	0.03 (0.07)	0.00	1.0000
Ant-eating Chat	0.04 (0.07)	0.04 (0.06)	0.00	1.0000
Buffy Pipit	0.01 (0.03)	0.01 (0.03)	0.00	1.0000
Blue crane	0.01 (0.03)	-		
Crowned Plover	0.13 (0.14)	-		
Eastern Long-billed Lark	0.16 (0.12)	-		
Spike-heeled Lark	0.06 (0.09)	-		
Pink-billed Lark	0.03 (0.06)	-		
Black Crow	0.07 (0.11)	-		
Sentinel Rock thrush	0.03 (0.04)	-		
Mountain Chat	0.04 (0.00)	-		
Buff-streaked chat	0.07 (0.11)	-		
Cloud Cisticola	0.01 (0.03)	-		
Pale-crowned Cisticola	0.01 (0.03)	-		
Levaillant's Cisticola	0.01 (0.03)	-		
Cape Wagtail	0.02 (0.05)	-		
Long-billed Pipit	0.07 (0.07)	-		
Plain-backed Pipit	0.03 (0.07)	-		
African Rock Pipit	0.01 (0.03)	-		
Cuckoo Finch	0.02 (0.05)	-		
Grey-winged Francolin *Francolinus africanus*	-	0.01 (0.02)		
Helmeted Guinea Fowl *Numida meleagris*	-	0.04 (0.10)		
Marsh Owl *Asio capensis*	-	0.01 (0.03)		
Common Waxbill *Estrilda astrild*	-	0.13 (0.31)		
Pin-tailed Whydah *Vidua macroura*	-	0.05 (0.11)		
All	0.63 (0.98)	0.56 (1.07)	0.59	0.5536

Table 2a. Distribution and number of nests found for each of the nine major grassland species in each of the three management systems (H+A = heavy grazing with annual burning, L+A = light grazing with annual burning, L+B = light grazing with biennial burning).

	Management system			
	H+A	L+A	L+B	
Species				Total nests
Grassveld Pipit	42	214	94	350
Yellow breasted Pipit	0	171	78	249
Orange-throated Longclaw	0	115	80	195
Ayres' Cisticola	0	123	35	158
Long-tailed Widows	0	67	69	136
Quail Finch	0	9	27	36
Common Quail	0	25	5	30
Rudd's Lark	0	11	0	11
Red-capped Lark	9	6	2	17
Total nests	51	741	390	1182

Table 2b. Paired *t*-test of differences in the means of nest density (±SD) for nine grassland bird species (Grassveld Pipit; Yellow-breasted Pipit; Orange-throated Longclaw, Ayres' Cisticola; Long-tailed Widow, Common Quail, Quail Finch, Rudd's Lark, and Red-capped Lark) nesting in heavily grazed (H+A) and lightly grazed grassland (L+B) in Wakkerstroom high-altitude grasslands. Nest density was calculated over 15 days periods (shortest time between re-nest).

Date	L+A (SD)	H+A (SD)	t	df	*P*	ln *P*
October 1-15	0.002 (0.004)	0.001 (0.002)	0.98	8	0.36	-1.02
October 16-31	0.005 (0.007)	0.001 (0.002)	1.34	8	0.22	-1.51
November 1-15	0.011 (0.011)	0.005 (0.008)	1.82	8	0.11	-2.21
November 16-30	0.028 (0.022)	0.010 (0.019)	2.03	8	0.08	-2.53
December 1-15	0.022 (0.018)	0.007 (0.009)	2.23	8	0.06	-2.81
December 16-31	0.031 (0.021)	0.004 (0.009)	3.06	8	0.02	-3.91
January 1-15	0.024 (0.016)	0.003 (0.006)	3.48	8	0.01	-4.61
January 16-31	0.027 (0.016)	0.001 (0.003)	3.30	8	0.01	-4.61
February 1-15	0.019 0.013 ()	0.002 (0.005)	3.00	8	0.02	-3.91
February 16-28	0.008 (0.005)	0.002 (0.005)	2.71	8	0.03	-3.51
March 1-15	0.001 (0.002)	0.000 (0.000)	1.32	8	0.22	-1.51
March 16-31	0.000 (0.001)	0.000 (0.000)	1.00	8	0.35	-1.05
Combined probability			**df, (P), -2∑lnP**	24	0.001	66.37

Table 2c. Paired *t*-test of differences in the means of nest density (±SD) for nine grassland bird species (Grassveld Pipit; Yellow-breasted Pipit; Orange-throated Longclaw, Ayres' Cisticola; Long-tailed Widow, Common Quail, Quail Finch, Rudd's Lark, and Red-capped Lark) nesting in annually burned (L+A) and biennially burned grassland (L+B) in Wakkerstroom high-altitude grasslands. Nest density was calculated over 15 days periods (shortest time between re-nest).

Date	L+A (SD)	L+B (SD)	*t*	df	*P*	ln *P*
October 1-15	0.002 (0.004)	0.005 (0.007)	-1.32	8	0.22	-1.51
October 16-31	0.005 (0.007)	0.019 (0.024)	-1.59	8	0.15	-1.90
November 1-15	0.011 (0.011)	0.038 (0.034)	-2.14	8	0.06	-2.81
November 16-30	0.028 (0.022)	0.039 (0.026)	-1.40	8	0.20	-1.61
December 1-15	0.022 (0.018)	0.027 (0.021)	-0.47	8	0.65	-0.43
December 16-31	0.031 (0.021)	0.032 (0.029)	-0.03	8	0.98	-0.02
January 1-15	0.024 (0.016)	0.013 (0.009)	1.94	8	0.09	-2.41
January 16-31	0.027 (0.016)	0.008 (0.006)	3.12	8	0.01	-4.61
February 1-15	0.019 (0.013)	0.017 (0.015)	0.33	8	0.75	-0.29
February 16-28	0.008 (0.005)	0.005 (0.006)	1.78	8	0.11	-2.21
March 1-15	0.001 (0.002)	0.001 (0.002)	-0.05	8	0.96	-0.04
March 16-31	0.000 (0.001)	0.001 (0.001)	-0.46	8	0.66	-0.42
Combined probability			**df, (P), -2∑lnP**	24	0.005	36.50

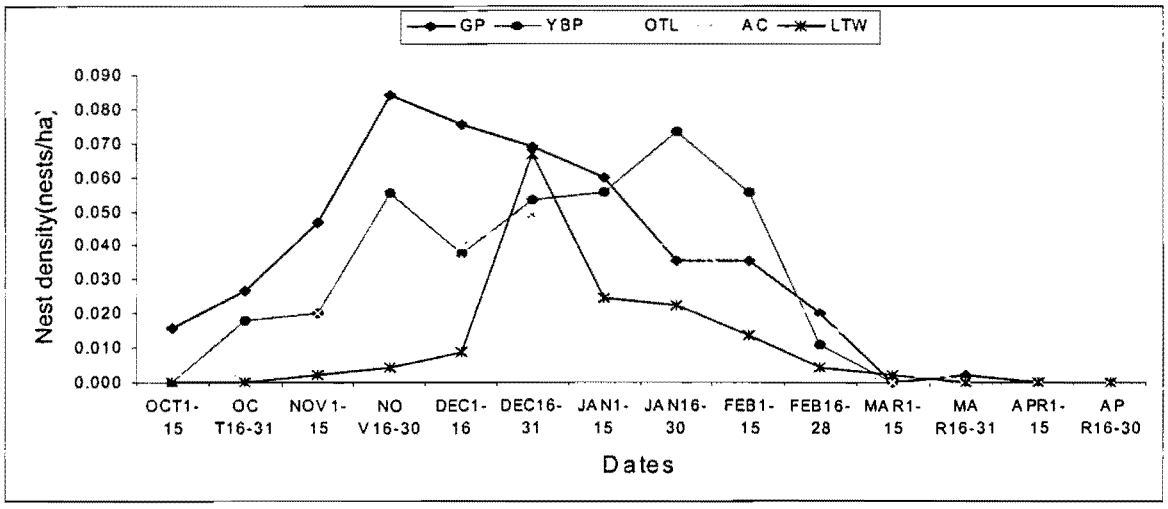

Fig 1. Nest densities of five focal species over 15-day periods during the breeding season in grassland under light grazing with frequent (annual) burning. Species: GP = Grassveld Pipit; YBP = Yellow-breasted Pipit; OTL = Orange-throated Longclaw, AC = Ayres' Cisticola; LTW = Long-tailed Widow.

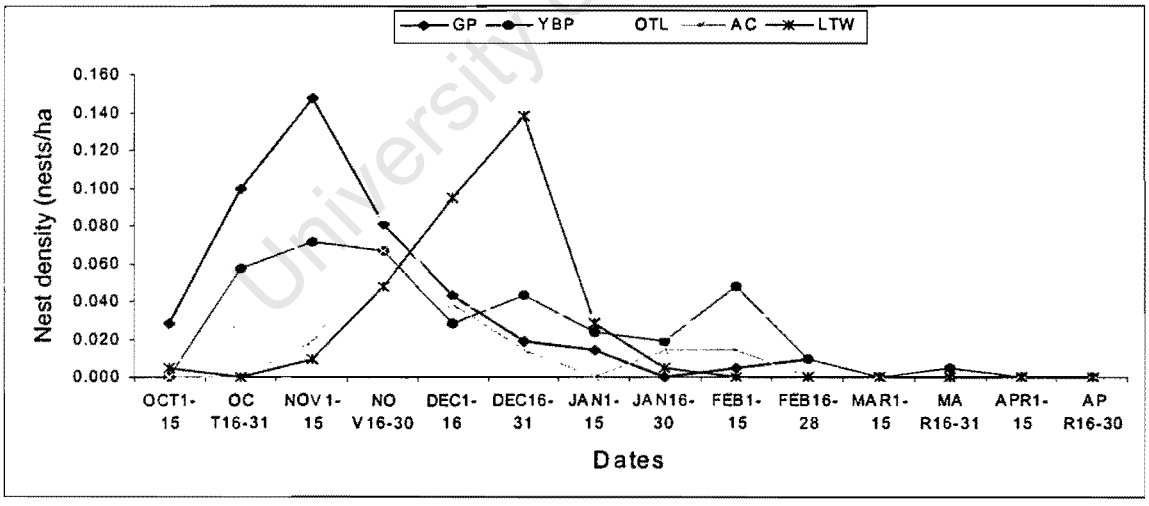

Fig 2. Nest densities of five focal species over 15-day periods during the breeding season in grassland under light grazing with infrequent (biennial) burning. Species: GP = Grassveld Pipit; YBP = Yellow-breasted Pipit; OTL = Orange-throated Longclaw, AC = Ayres' Cisticola; LTW = Long-tailed Widow.

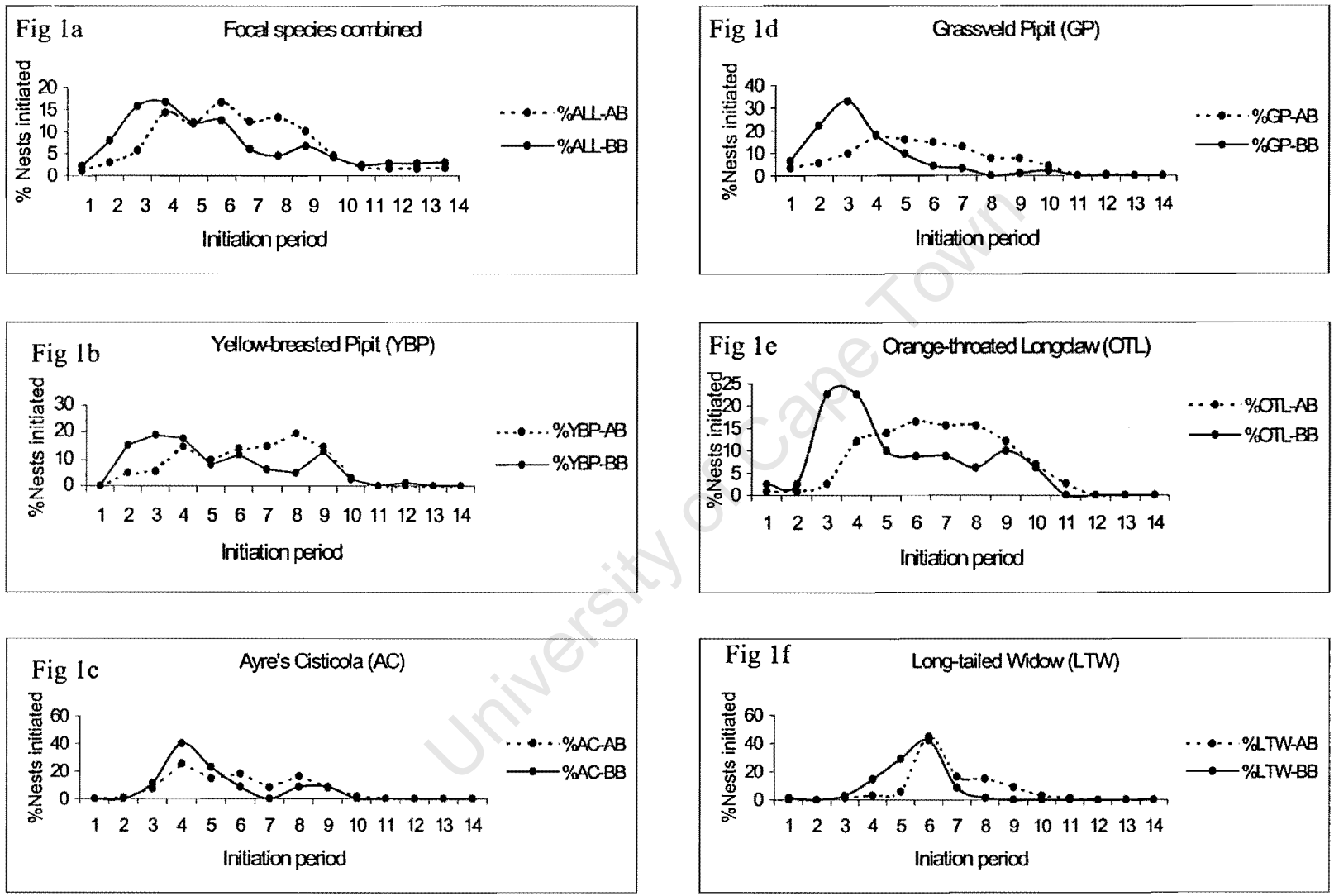

Fig3. (a-f). Nest chronology of clutch initiation among five major grassland bird species in grasslands under annual burning (AB) and under biennial burning (BB) regimes during each of the thirteen 15-days blocks spanning the breeding season; starting on 01 October.

Effects of management practices on clutch size

Only GP provided a sufficient sample size to test for the effect of grazing intensity on clutch size. Clutch size for GP was significantly smaller in heavily grazed (2.27 ± 0.52) than in lightly grazed grasslands (2.89 ± 0.57) (t-test: $t = 6.17$, df = 197, $P < 0.001$). When I controlled for grazing, I found that clutch size for LTW was significantly smaller in annually burned grassland (3.02 ± 0.67) than in biennially burned grassland (3.41 ± 0.53) (t-test: $t = 3.40$, df = 109, $P < 0.001$). I found no effect of burning on any of the other 6 species (Table 3, $P > 0.05$). Management practices can influence clutch size in two ways, viz. food availability and nest predation. When I controlled for predation by considering clutch size in L+A and L+B grasslands where risk of predation for GP were equal (0.958 ± 0.004 versus 0.965 ± 0.005; Chi-Square; χ^2, = 1.19, 1df, $P > 0.05$), burning frequency had no effect on clutch size (t-test: $t = -0.40$, df = 240, $P > 0.05$) (2.89 ± 0.52) versus 2.92 ± 0.56). However, when I controlled for food by considering clutch size in H+A and L+B grasslands where food abundance were equal (12.6 ± 5.0 g versus 16.9 ± 9.6 g; Mann-Whitney U test, $U = 430$, 66 df, $P > 0.05$), clutch size for GP was significantly smaller in heavily grazed (2.27 ± 0.57) compared to lightly grazed grasslands (2.92 ± 0.56) (t-test: $t = 5.51$, df = 107, $P < 0.0001$).

Number of broods

Although some birds were colour banded, most birds in this study were not individually identifiable. Banded birds, however, indicated that some pairs were rearing at least two broods per season and regularly re-nested after a failed attempt. Multiple broods and re-nesting to replace depredated nests occurred in YBP, GP, and OTL and were also a possibility for all other species. Three successful broods per breeding season were occasionally possible for early nesters.

Table 3. Mean clutch size (SD) of seven grassland bird species nesting in annually (L+A) versus biennially burned (L+B grasslands, but under similar light grazing pressure from livestock.

		Mean (±SD)	Mean (±SD)			
	n	L+A	L+B	t-value	df	p
Long-tailed Widow	(52, 59)	3.02 (0.67)	3.41 (0.53)	-3.40	109	0.0010
Ayre's Cisticola	(94, 25)	3.48 (0.67)	3.52 (0.59)	-0.28	117	0.7789
Grassveld Pipit	(166, 76)	2.89 (0.52)	2.92 (0.56)	-0.40	240	0.6886
Yellow-breasted Pipit	(117, 55)	3.02 (0.44)	3.02 (0.36)	-0.02	170	0.9872
Orange-throated Longclaw	(81, 58)	3.26 (0.67)	3.16 (0.45)	1.03	137	0.3042
Quail Finch	(09, 25)	4.44 (0.88)	4.08 (0.95)	1.00	32	0.3243
Common Quail	(25, 04)	5.92 (1.41)	4.75 (2.06)	1.45	27	0.1585

DISCUSSION

I found that vegetation cover, structure (foliage density), complexity and structural heterogeneity were lowest in H+A grasslands, intermediate in L+A grasslands and highest in L+B grasslands (Chapter 2). This result hinted at the fact that grazing and burning may affect vegetation, and consequently abundance or availability of food resources and nesting sites for breeding birds.

Species richness is affected by excessive and regular defoliation

As expected, management practices affected species richness and diversity suggesting that grazing pastures varied considerably in their attractiveness for birds. The low species richness in H+A grasslands could be explained by the simplicity of the vegetation structure in them. Burning eliminates ground litter, reduces habitat heterogeneity and simplifies habitats floristically and structurally, which in turn can reduce the diversity of birds. This is probably due to the effects of grazing and burning on availability of seeds and invertebrate food resources. Low disturbance (e.g. in L+B grasslands) may, however, also lead to a decline in species diversity. For example, this study found that all birds avoided tall and thick vegetation suggesting that the exclusion of grazing and burning as management tools in grassland can be detrimental to the associated bird fauna. This supports the intermediate disturbance hypothesis (see Vitousek and Hooper 1993). Many studies elsewhere have also demonstrated that species number is often greatest under moderate disturbance (see references in Pickett and White 1985). Our results further indicate that birds species diversity is likely to drop under high disturbance supporting the hypothesis that range contractions (or local extinctions) of grassland birds such as the Yellow-breasted Pipit, are a consequence of changing management practices on grasslands.

Bird abundance is affected by management-related defoliation by management practices

Bird densities were significantly higher for all species in lightly grazed compared to heavily grazed grasslands, but there was no difference in this respect between annually burned and biennially burned grasslands. Although I recorded 48 species during the study period, fewer than 10 species could be considered as common. Higher abundance of birds in L+A than H+A grasslands suggests that breeding grassland birds may not tolerate excessive disturbance. The observed low density in H+A grassland could be explained

either by food limitation or nest predation because heavy grazing can reduce availability of food (Conner *et al.* 1986) or nesting substrates (Morris 1967, Ammon and Stacey 1997). Higher abundance of birds in L+A than in L+B grasslands suggests that breeding grassland birds may, however, prefer some disturbance. I did not rigorously test the effect of total removal of grazing or the complete exclusion of burning. However, two plots that were only lightly grazed and not burned for three years were generally avoided by most of the species, suggesting a bell shape in relation to species response to management disturbance. Our results are consistent with the hypothesis that an increase in intensity of grazing and frequent burning is the cause of the observed decline in densities of grassland birds (e.g. see Saab *et al.* 1995, Bendell 1974). Further, moderate grazing and infrequent burning appear to be most beneficial to grassland birds. Ideally, grasslands should be burned biennially and grazed moderately in order to benefit grassland bird populations. Although the total bird diversity and density was reduced by frequent burning and intense grazing, individual species were variously positively, negatively or neutrally affected by management regimes. For example, RCL preferred open areas created by heavy grazing. GP appeared resilient to grazing and appeared to tolerate, adapt and cope with the different intensity and levels of grazing and burning. Most birds were more than twice as abundant in lightly grazed than in heavily grazed grassland indicating their sensitivity to vegetation changes resulting from livestock grazing. The Yellow-breasted Pipit (vulnerable) was most affected by the level of disturbance. These observations suggest that, conservation plans need a management approach that considers individual species, or management for habitat mosaics for multiple-species conservation. Other studies have shown similar patterns in bird responses to management regimes (e.g. see Zimmerman 1992, 1993, Saab *et al.* 1995, Henderson *et al.* 2000, Muchai *et al.* 2002).

Nest density relates to management practices

Even though most bird species were present in all of the management regimes, most only nested in specific habitats indicating that their distribution may largely be constrained by lack of suitable nesting substrates or other resources for breeding. Grazing and burning may affect vegetation, and consequently availability of nesting sites for breeding birds. Vegetation structure influences the placement of nests (see Martin 1993c, Chapter 4). Low ground cover and foliage density might be unsuitable to foliage dependant-species. For example, H+A grassland, which was notable for its sparse vegetation cover and structure,

was avoided for breeding by most of the focal species. YBP and OTL showed the strongest affinities for dense vegetation cover for nesting in. Choices of nesting habitat by the species in this study are consistent with the prediction that birds would avoid habitats that are more vulnerable to predation for breeding purposes. Small passerines, especially in the tropics, are particularly vulnerable to predators (Ricklefs 1969) and dense vegetation may enhance their nesting success (Martin and Roper 1988, Chapter 5). Indeed, the relatively low number of nests that we recorded in H+A grasslands could either suggest that birds avoids nesting there, or that there was a high probability of nests being trampled, abandoned or lost to predators before we found them. Although nest densities were similar when comparing L+A and L+B grasslands, I could have missed finding more nests in the former due to higher predation rates there.

Life history and duration of breeding

Breeding commenced earlier in biennially burned than in annually burned grasslands. Early nesters are at an advantage as they have a longer nesting season. The delay in clutch initiation may be costly if seasonal declines in nesting condition occur. Birds nesting in habitats where risk of predation is intense can offset this effect by extending the duration of breeding or laying multiple broods. The delay in clutch initiation may reduce the number of broods by successful pairs or the opportunities for re-nesting. Multiple broods and re-nesting were observed in the few identified breeders. Although few birds were banded, multiple broods and re-nesting could have been a common phenomenon based on the fact that after nest failure or successful breeding, new nests were frequently found near earlier ones.

Clutch size is affected by management practices

Although the proximate mechanism by which clutch size is adjusted remains poorly understood, clutch size generally is one of the traits showing close proximate adjustments to individual and local conditions (Lack 1968). Traditionally, evolution of clutch size has long been mainly attributed to food limitation (Lack 1947) or to a combination of several life-history traits (Roff 1992, Stearns 1992, Murphy 2000). However, although often overlooked, nest predation is the primary cause of nest mortality for many bird species (Ricklefs 1969, Chapter 2), and may be the main driving force influencing avian life histories (Skutch 1949, Linden and Møller 1989, Martin 1996, Julliard et al., 1997, Martin

et al. 2000a). My results are in accordance with these latter studies, which attributes variation of clutch size to predation. Taken together, my results add support to the idea that although frequently underrated, nest predation may be a more important force in driving evolution of avian clutch size than food. Species that feed their dependent altricial young may reduce risk of nest predation to their nestlings by reducing the rate that they visit the nest to feed their young (Ghalambor and Martin 2001), thus trading the cost linked with reduced food delivery to their offspring against a reduction in risk of death to themselves or their young ones (Ghalambor and Martin 2001). Large clutches should require more feeding trips by parents to feed young. Increased activities associated with large broods may attract predators. (Skutch 1949, Martin *et al.* 2000a, Murphy 2000).

Note that young birds may have used marginal habitats as opposed to older birds. If suitable habitats are already saturated, immature birds could be forced into low quality habitats (H+A), both in terms of food availability and risk of nest predation. If older birds occupy the best nesting habitats, then higher clutch sizes in high quality plots may simply be a result of the positive correlation with bird quality. This could also explain the reduced clutch size for GP in H+A grassland and for LTW in L+A grasslands. However, on occasion first year breeders (young birds) had territories in high quality habitats suggesting that habitats were not saturated.

4

Effects of management practices on grassland birds habitat selection: Is nest site preference under selection and adaptive?

Abstract

Identification of traits determining fitness and knowledge of the ecological significance of traits under selection is crucial for understanding the way in which organisms choose their habitats. I examined microhabitat choices, and the form of natural selection and adaptiveness of preferences of four coexisting grassland bird species, which breed in the high altitude grasslands, at Wakkerstroom South Africa. Breeding birds selected nest patches with greater foliage cover, vegetation density, and heterogeneity than was generally available. The non-random nest site choices differed among species. Comparison of vegetation features at successful and unsuccessful nests supported the idea that nesting success is a strong selective force on habitat choice. Nest success was higher in preferred than non-preferred habitat for all the three species, suggesting that preferences were adaptive. Estimation of fitness functions relating fitness of individuals to critical habitat features using cubic spline regressions, standardized directional selection differentials and selection gradients suggest that natural selection might be acting to favor preference for specific habitat features that determines fitness.

Key words: South African high altitude grasslands, management practices, habitat selection, natural selection, critical habitat features.

INTRODUCTION

Nest-site microhabitat choices are assumed to be adaptive such that fitness is greater in preferred than non-preferred microhabitats (Jaenike and Holt 1991), and to have a genetic basis (Kekick *et al.* 1980, Jaenike and Holt 1991). That is, when allowed complete freedom to choose habitats, birds should choose a habitat in which fitness is maximized. Genetic variation for habitat selection is common, particularly in invertebrates (Kekick *et al.* 1980, Jaenike and Holt 1991), but not so in vertebrates (Schluter 1988). Identification of specific habitat features that influence the occurrence, distribution, density, and fitness of birds is a major goal in avian ecology (Holmes 1981). When birds settle in habitats and select nesting

patches, they are believed to do so non-randomly (e.g. see, Fretwell 1972, Mackenzie and Sealy 1981, Cody 1985, Peterson and Best 1985, Martin and Roper 1988, Rosenzweig 1991, Rodrigues 1994). Explanations for why individuals are not randomly distributed across habitat types, however, remain poorly understood.

Density may not be positively correlated with fitness (Pulliam 1988, Martin 1998) or reflect preference (Van Horne 1983). Yet, traditionally, habitat preferences in birds are often inferred from correlations of occurrence and density to habitat features (e.g. see Fretwell 1972, Cody 1985, Muchai *et al.* 2002) rather than measurements that have a direct fitness component. Recently, Martin (1998) has shown that nest-site selection is closely tied to fitness and has potential consequences for natural selection and population dynamics. Fitness and habitat choice in birds is commonly measured at the population level (Fretwell and Lucas 1970). However, nest sites represents microhabitat choice by individuals. Thus, measurements of fitness consequences of nest sites choices by individuals provide the most appropriate test of habitat preference.

Adaptiveness of habitat preferences in birds can be examined by estimating the relative fitness of habitat choices by individual breeding birds when each individual is given the full range of habitats from which to choose (Jaenike and Holt 1991, Martin 1998). I had the opportunity to study grassland birds in a system that was managed in three ways, viz. heavily grazed and burned annually (H+A), lightly grazed and burned annually (L+A), and lightly grazed and burned every second year (L+B). Vegetation varied considerably between management regimes providing a gradient in variation in habitat features across management types. Since birds were nesting in these habitat gradients, and because habitat features are known to directly influence fitness (Martin 1993c), differentially managed grassland areas provided me with an ideal opportunity to examine nest-site selection and adaptiveness of microhabitat preferences in birds. Birds were breeding in the different management types at different densities because of the structurally dissimilar habitat types caused by differential management (Chapter 3). Relative breeding densities in these management habitat types were thus assumed to represent preferences.

In this paper, I set out to examine nest site choices and whether they are under selection and adaptive in a grassland study system using four ground-nesting grassland bird species. First, I show that habitat features at nest site differed with those at random sites and between species. Second, I compare vegetation features for successful versus failed nests to examine whether they differ in order to identify critical nest site habitat features for

each species. Third, I document preferences by examining the nesting densities of birds across management systems. Fourth, I analyze various components of fitness to examine adaptiveness of preferences. Fifth, I estimate the selection functions to examine whether selection gradients could favour and maintain preferences.

STUDY AREA AND METHODS

Study area

The study was conducted in the high altitude grasslands of Wakkerstroom in Mpumalanga province, South Africa at 1800-2200 m a.s.l. from 1998-2001. The study area (centred at 27° 10' S, 30° 06' E) is located on the high lying grassveld between 1800m to 2250m elevations. The main land use in the Wakkerstroom district is large-scale livestock farming. The grasslands are managed with grazing and burning. More than 80% of the farmers either entirely rear beef cattle. Other farmers practice mixed farming of both cattle and a few sheep. Farmers also keep some goats, a few horses and game such as blesbok. Grazing intensity is mainly either heavy or light. Heavy grazing intensity was assumed to be > 3 cow (454 kg) or 5 sheep/ha and light grazing was < 1.5 cow (454 kg) or 5 sheep /ha. Livestock continuously graze the same grassland throughout the breeding season. The grasslands are burned either annually or biennially.

Four study species of ground-nesting grassland birds were used in this study, viz. Yellow-breasted Pipit *Hemimacronyx chloris* (YBP), Grassveld Pipit *Anthus cinamomerous* (GP), Orange-throated Longclaw *Macrony capensis* (OTL), and Ayres' Ayres' Cisticola *Cisticola ayressii* (AC). Multiple brooding and re-nesting are common in all these species and they all build a new nest in a different location on the territory for each nesting attempt. YBP, GP and OTL are all members of the family Motacillidae, and considered to be ecologically broadly similar.

Field work

The whole study area was intensively searched for nests (for all grassland birds) throughout the study period from 1998 to 2001. Searching and locating of nests was done by rope dragging to flush out birds from nests, or based on behavioural observation. This method of nest finding (as opposed to direct searching) minimizes biases of finding nests that are easily detectable. Nests were visited to record their status at 1-5 day intervals until the

event was completed or had been terminated. Nests were considered successful if one or more young fledged, and unsuccessful if they failed completely.

Microhabitats were measured following techniques modified from Wiens and Rotenberry (1981). Briefly, vegetation was measured at nest sites, and for comparison, at random sites. Random sites were the same measurements recorded for each management treatment (see Chapter 2). The nest site was considered to be all habitats from 1 m to 10 m from the nest. Vegetation features at nest site were measured at 1m intervals along a 10m tape extending outwards from the nests in each of the four cardinal directions. Nest site vegetation measurements were recorded using the same protocol as described in Chapter 2. 10 nest site and 10 random site vegetation variables were recorded.

DATA ANALYSIS

Nests were discovered at various stages of development. Thus, daily nest success rate was calculated following Mayfield (1961, 1975), which only make use of information from the period during which a nest was under observation. The mid-point between nest visits was used to estimate when critical events in the nesting cycle occurred. Half the number of days between subsequent visits over which a nest failed or fledged (although we did not extrapolate beyond the normal nesting period) was added to the previous number of days the nest survived to obtain the total exposure days (Mayfield 1961). For each species, I calculated daily mortality as the number of failures divided by the total number of active nest observation days (exposure days). I calculated daily survival as (1 - daily mortality). I calculated standard errors of Mayfield's survival probabilities according to Johnson (1979) and variance of Mayfield's estimator according to Hensler and Nichols (1981). Hypothesis testing was conducted using the Z-test for daily survival probability according to Hensler and Nichols (1981) and Program CONTRAST (Hines and Saucer 1989).

I used univariate analysis of variance to test for differences in the vegetation characteristics between nest site and random sites, and variation in vegetation variables between successful and unsuccessful nest sites for each bird species. These univariate comparisons involved 1-way ANOVA. I compared each species' nest site with available habitat (random sites) in separate analysis for all 10 habitat variables. Habitat variables that discriminated between groups (nest site versus random sites, and successful versus unsuccessful nest sites) were identified by stepwise discriminant function analysis (SDFA). Equality of the covariance matrices was tested using Box's *M* criterion. The between group

variance/covariance matrices often showed significant heteroscedasticity ($P < 0.05$). Thus, discriminant function was based on the pooled within-group covariance matrices and using the Mahalanobis distance (Minimum D^2) between group centroids as the criterion for maximizing separation of groups (Hand 1981, Williams 1983). This method is most appropriate when covariance matrices are not homogenous (Hand 1981, Williams 1983). However, moderate violations of equality of the covariance matrices probably have little effect on two-group classification success and *F*-tests can still be powerful (Cooley and Lohnes 1971, Williams 1983). Thus, Wilks' lambda and *F*-tests were used to determine the combination of variables providing the best group separation for two-group classifications. Because group size sample sizes differed, the classification performance of SDFA was tested against a chance model, using Cohen's kappa statistic (Z values) to test whether the SDFA models classified the observations significantly better than chance alone (Titus *et al.* 1984). Structure coefficient from DFA was used to determine correlations of variables with the discriminant functions and standardized coefficients to determine the unique (partial) contribution of each variable to the discriminant functions.

The form of natural selection on habitat selection was estimated by estimating selection surfaces (fitness function) relating nest survival of individuals to habitat variables that influence nest site choices. Fitness functions, *f*, were estimated using cubic spline regression (Schluter 1988), a 'non-parametric' technique, applied to successful versus unsuccessful vegetation binomial data using the equation: $Y = f(z)$ + random error, where, Y is survival (nesting success; 1 or 0 for success or failure respectively). A measure of individual fitness, z is the trait (continuous variable) under selection and $f(z)$ is the probability of survival as a function the selected trait. Confidence limits (standard errors of the predicted regression surfaces) for splines were estimated by bootstrapping in which the original data was re-sampled 200 times (Schluter 1988). Natural selection is defined as variation in fitness. Therefore relative selection intensity, which is a function of intrapopulation variation in fitness, was estimated as the coefficient of variation of relative fitness. Critical habitat variables that differentiated successful nests from unsuccessful nests for each species were assumed to be the phenotypic traits influencing variation in fitness, thus preference, and were used in the analysis of relative selection intensity. Selection differentials (s), which measure phenotypic responses to selection on correlated traits, were estimated as the slope of the univariate regression of relative fitness on standardized characters. Phenotypic characters were direct measures of critical vegetation

variables. The assumption here was that vegetation measurements reflected phenotypic variation in behavioural choices on which selection acts (see Jaenike and Holt 1991). Standardized directional selection gradients *(B)* were estimated as the partial regression coefficients of relative fitness versus all important habitat variables. Habitat variables used in these analyses seemed to be directly used by the study birds.

I performed all the statistical analysis using the STATISTICA software (StatSoft Inc, 2000) unless stated otherwise. Analyses for computation of fitness surfaces were done by a software (Univariate program version 4.0) provided by Dolph Schluter. Significant levels for statistical tests were set at $P < 0.05$. Percentage data were arc sine transformed to more closely fit the normal distribution (Sokal and Rohlf 1995). Means are presented ± SD.

RESULTS

Vegetation differences among nest sites and random sites

Nest sites differed from random sites for most of the 10 habitat variables examined for all the four species (Appendix 1), with random sites having the lowest values, indicating nonrandom nest-site choice. All four discriminant analyses (see tables 1-4) yielded a single highly significant canonical axis ($P < 0.0001$ for all cases) that strongly differentiated nest sites from random sites, further supporting the non-random nest site selection (Mahalanobis distance: $P < 0.0001$ for all cases). Briefly, all the four species' nests were typically placed in areas with relatively more ground vegetation cover, higher vegetation structure (foliage density and height), and greater heterogeneity than available elsewhere. One could confidently distinguish YBP nest sites from random sites using three out of the 10 habitat variables (Table 1), including two horizontal heterogeneity variables and one vertical heterogeneity (patchiness) variable (Table 1). OTL nest sites were distinguished from random sites using six out of the 10 habitat variables (Table 2), including one coverage variable, two structural vegetation variable (horizontal and vertical foliage density), and three horizontal heterogeneity variables (Table 2). One could distinguish GP nest sites from random sites with five of the 10 habitat variables (Table 3), including one coverage variable, one structural vegetation variable (vertical foliage density), one vertical patchiness variable and two horizontal heterogeneity variables (Table 3). Lastly, AC nest sites were differentiated from random sites using six out of the 10 habitat variables (Table 4), including one coverage variable, two structural vegetation variable (horizontal and vertical foliage density), and three horizontal heterogeneity variables (Table 4).

Nest patch differences among species

SDFA yielded two highly significant ($\chi^2 > 12.8$, $P < 0.05$ in both cases) canonical axes that strongly differentiated nest sites of the three ecologically similar species from each other (Mahalanobis: $P < 0.05$, $F > 2.7$, df = 5, 444 for all pairwise comparisons). Nest sites of the three species were correctly classified more frequently than not (Table 5), reflecting strong differences in nest-site selection. When all four species were considered, SDFA yielded two highly significant discriminant function axes ($\chi^2 > 114.41$, $P < 0.0001$ in the first two canonical axes) that strongly differentiated nest sites of the four species from each other (Mahalanobis: $P < 0.05$, $F > 2.4$, df = 7, 555 for all pairwise comparisons) and one non-significant canonical axis ($\chi^2 = 9.9$, $P > 0.05$). Nest sites of the four species were correctly classified more frequently than not (Table 6), reflecting strong differences in nest-site selection between species.

Table 1. Mean (SD) habitat characteristics that are important in discriminating between (A) nest site versus random site and (B) successful versus failed nests of the Yellow-breasted Pipit, using univariate (ANOVA) of differences in the means and stepwise discriminant function analysis. Variables are given in the order in which they were entered in the model. Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

		Univariate analysis				Discriminant analysis			
A	Variable	Nest Site (150)	Random (54)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	*P*
	HFD10	5.77 (2.12)	2.07 (1.58)	137.25	0.0001	0.537	-0.585	-1.114	0.0001
	CVTOTHITS	0.52 (0.14)	0.82 (0.32)	88.21	0.0001	0.534	0.470	0.994	0.0001
	VFD10	4.36 (1.78)	1.33 (1.48)	124.37	0.0001	0.341	-0.558	0.214	0.0072
	Correctly classified Z = 9.79***	100.0%	87.0%				Eigenvalue	1.981	
B		Successful (83)	Failed (67)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	P
	MAXHGT	26.9 (9.2)	17.41 (6.3)	51.77	0.0001	0.779	0.925	0.680	0.0002
	VFD10	4.92 (1.63)	3.65 (1.72)	21.38	0.0001	0.728	0.594	0.310	0.0564
	CVMAXHGT	0.47 (0.12)	0.59 (0.14)	30.00	0.0001	0.720	-0.704	-0.265	0.1475
	Correctly classified Z = 6.01***	73.5%	76.1%				Eigenvalue	0.409	

MAXHGT = mean maximum vegetation height; CVMAXHGT (coefficient of variation of the maximum height) = a measure of horizontal heterogeneity; CVTOTHITS (coefficient of variation of the mean total number of hits) = a measure of horizontal heterogeneity; HFD10 = horizontal foliage diversity; and VDF10 = vertical foliage diversity.

Table 2. Mean (SD) habitat characteristics that are important in discriminating between (A) nest site versus random site and (B) successful versus failed nests of the Orange-throated Longclaw, using univariate (ANOVA) of differences in the means and stepwise discriminant function analysis. Variables are given in the order in which they were entered in the model. Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

		Univariate analysis				Discriminant analysis			
A	Variable	Nest Site (131)	Random (54)	F	P	Wilk's lambda	Structure coefficient	Standard coefficient	P
	HFD10	5.28 (2.44)	2.07 (1.58)	79.72	0.0001	0.629	-0.506	-1.125	0.0001
	CVTOTHITS	0.54 (0.26)	0.82 (0.32)	39.56	0.0001	0.495	0.357	0.798	0.0001
	HIT0-10	6.54 (3.29)	3.52 (1.88)	40.01	0.0001	0.427	-0.359	-1.340	0.0001
	TOTHITS	19.40 (17.46)	5.63 (5.41)	32.23	0.0001	0.418	-0.322	1.218	0.0001
	%TGCOV	96.9 (23.5)	97.3 (11.2)	0.48	0.4875	0.393	0.040	0.393	0.0012
	CVMAXHGT	0.51 (0.18)	0.57 (0.11)	6.29	0.0130	0.379	0.142	0.287	0.0527
	Correctly classified Z = 9.50***	99.2%	83.3%				Eigenvalue	1.695	
B		Successful (69)	Failed (62)						
	HIT0-10	7.71 (3.79)	4.65 (1.20)	32.38	0.0001	0.778	-0.828	-1.684	0.0058
	%HCOV	7.9 (5.9)	10.9 (8.7)	5.38	0.0219	0.788	0.338	0.867	0.0023
	CVMAXHGT	0.48 (0.19)	0.59 (0.32)	5.52	0.0203	0.759	0.554	0.484	0.0327
	%GCOV	88.8 (22.4)	83.0 (22.1)	8.38	0.0045	0.760	-0.421	0.674	0.0292
	TOTHITS	25.82 (20.82)	11.39 (8.79)	25.64	0.0001	0.747	-0.737	0.910	0.1148
	Correctly classified Z = 5.23***	79.7%	66.1%				Eigenvalue	0.366	

%GCOV = percentage grass cover; %HCOV = percentage herb cover; %TGCOV) = percentage total ground cover; MAXHGT = mean maximum vegetation height; HIT0-10 = mean horizontal foliage density; TOTHITS = mean vertical foliage density; CVMAXHGT (coefficient of variation of the maximum height) = a measure of horizontal heterogeneity; CVTOTHITS (coefficient of variation of the mean total number of hits) = a measure of horizontal heterogeneity; and HFD10 = horizontal foliage diversity.

Table 3. Mean (SD) habitat characteristics that are important in discriminating between (A) nest site versus random site and (B) successful versus failed nests of the Grassveld Pipit, using univariate (ANOVA) of differences in the means and stepwise discriminant function analysis. Variables are given in the order in which they were entered in the model. Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

		Univariate analysis				Discriminant analysis			
(a)	Variable	Nest Site (170)	Random (54)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	*P*
	HFD10	6.34 (2.65)	2.07 (1.58)	126.38	0.0001	0.794	-0.605	-1.684	0.0001
	CVTOTHITS	0.67 (0.26)	0.82 (0.32)	12.23	0.0006	0.629	0.188	1.251	0.0001
	VFD10	3.00 (1.89)	1.33 (1.48)	35.09	0.0001	0.479	-0.319	1.142	0.0001
	TOTHITS	10.90 (13.93)	5.63 (5.41)	7.34	0.0073	0.413	-0.146	-0.462	0.0005
	%TGCOV	94.3 (23.0)	97.4 (11.2)	11.83	0.0007	0.401	0.185	-0.236	0.0190
	Correctly classified Z = 9.83***	98.8%	87.0%				Eigenvalue	1.558	
(b)		Successful (81)	Failed (89)						
	MAXHGT	21.03 (9.44)	12.89 (5.76)	46.93	0.0001	0.719	-0.819	-0.375	0.0764
	HIT0-10	5.81 (3.59)	3.24 (1.09)	41.43	0.0001	0.775	-0.769	-2.319	0.0001
	TOTHITS	16.14 (18.53)	6.13 (3.41)	25.02	0.0001	0.763	-0.598	2.224	0.0003
	VFD10	3.00 (1.89)	1.33 (1.48)	35.09	0.0001	0.744	-0.350	-0.678	0.0029
	Correctly classified Z = 6.70***	72.8%	78.7%				Eigenvalue	0.417	

%TGCOV) = percentage total ground cover; HIT0-10 = mean horizontal foliage density; TOTHITS = mean vertical foliage density; CVMAXHGT (coefficient of variation of the maximum height) = a measure of horizontal heterogeneity; CVTOTHITS (coefficient of variation of the mean total number of hits) = a measure of horizontal heterogeneity; HFD10 = horizontal foliage diversity; and VDF10 = vertical foliage diversity.

Table 4. Mean (SD) habitat characteristics that are important in discriminating between (A) nest site versus random site and (B) successful versus failed nests of the Ayre's Cisticola, using univariate (ANOVA) of differences in the means and stepwise discriminant function analysis. Variables are given in the order in which they were entered in the model. Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

		Univariate analysis				Discriminant analysis			
(a)	Variable	Nest Site (62)	Random (54)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	*P*
	HFD10	4.91 (2.31)	2.07 (1.58)	58.13	0.0001	0.757	-0.422	-1.747	0.0001
	CVTOTHITS	0.61 (0.19)	0.82 (0.32)	18.49	0.0001	0.358	0.239	0.921	0.0001
	VFD10	1.80 (1.46)	1.33 (1.48)	2.89	0.0916	0.262	-0.085	-0.172	0.6287
	TOTHITS	7.72 (5.67)	5.63 (5.41)	4.09	0.0455	0.314	-0.104	2.221	0.0001
	HIT0-10	4.81 (1.49)	3.52 (1.88)	17.14	0.0001	0.307	-0.223	-1.163	0.0001
	%TGCOV	97.3 (17.6)	97.3 (11.2)	0.00	0.9711	0.268	-0.010	0.206	0.1073
	Correctly classified Z = 9.72***	98.3%	96.3%				Eigenvalue	2.821	
(b)		Successful (39)	Failed (23)						
	HIT0-10	4.99 (1.55)	3.47 (0.89)	18.26	0.0001	0.934	-0.864	-0.907	0.0001
	CVTOTHITS	0.58 (0.19)	0.68 (0.18)	4.58	0.0364	0.776	0.427	0.506	0.0421
	Correctly classified Z = 2.59**	87.2%	47.8%				Eigenvalue	0.387	

%TGCOV) = percentage total ground cover; HIT0-10 = mean horizontal foliage density; TOTHITS = mean vertical foliage density; CVMAXHGT (coefficient of variation of the maximum height) = a measure of horizontal heterogeneity; CVTOTHITS (coefficient of variation of the mean total number of hits) = a measure of horizontal heterogeneity; HFD10 = horizontal foliage diversity; and VDF10 = vertical foliage diversity.

Table 5. Classification of nest sites (number and percentage of nests classified as nests of each species) from discriminant functions of the three ecologically similar species of the family Motacillidae based on separate covariance matrices.

	Predicted species			
Actual species	Orange-throated Longclaw	Grassveld Pipit	Yellow-breasted Pipit	Total
Orange-throated Longclaw	44 (33.6%)	32 (24.4%)	55 (42.0%)	131
Grassveld Pipit	23 (13.5%)	117 (68.8%)	30 (17.6%)	170
Yellow-breasted Pipit	29 (19.3%)	38 (25.3%)	83 (56.3%)	150
Total	96	187	168	451

Table 6. Classification of nest sites (number and percentage of nests classified as nests of each species) from discriminant functions of all four the study species based on separate covariance matrices.

	Predicted species				
Actual species	Ayre's Cisticola	Orange-throated Longclaw	Grassveld Pipit	Yellow-breasted Pipit	Total
Ayre's Cisticola	60 (52.6%)	7 (6.1%)	34 (29.8%)	13 (11.4%)	114
Orange-throated Longclaw	11 (8.4%)	39 (29.8%)	30 (22.9%)	51 (38.9%)	131
Grassveld Pipit	17 (10.0%)	17 (10.0%)	107 (62.9%)	29 (17.1%)	170
Yellow-breasted Pipit	8 (5.3%)	21 (14.0%)	40 (26.7%)	81 (54%)	150
Total	96	84	211	174	565

Vegetation differences between successful and unsuccessful nest sites

Vegetation variables associated with successful nests differed from those associated with unsuccessful nesting attempts for all species (Appendix 1). Generally, individuals with successful nesting attempts chose nest patches with greater vegetation cover, higher foliage density, greater vertical heterogeneity and lower horizontal heterogeneity than unsuccessful individuals. All four discriminant analyses (see Table 1-4) each yielded a single highly significant discriminant function axis ($P < 0.0001$ for all cases) that strongly differentiated successful nests from unsuccessful nests (Mahalanobis distance: $P < 0.0001$ for all cases). Successful YBP nests tended to be placed in areas with a combination of less horizontal heterogeneity and greater vertical patchiness than unsuccessful ones (Table 1). In addition, vegetation was taller at successful YBP nests than failed nests (Table 1). Successful OTL nests were associated with greater horizontal foliage density and lower horizontal vegetation heterogeneity than failed ones (Table 2). In addition, grass cover for successful OTL nests were significantly higher, and herb cover was significantly lower, at successful nests than failed nests (Table 2). Successful GP nests were generally placed in vegetation with greater horizontal and vertical foliage density and greater vertical structure and heterogeneity than failed ones (Table 3). In addition, vegetation was taller at successful GP nests than failed nests (Table 3). Successful AC nests generally were placed in vegetation with greater horizontal foliage density and lower horizontal heterogeneity (Table 4).

Microhabitat preferences

Vegetation characteristic varied with management treatment (Chapter 2). Vegetation cover, structure and heterogeneity were lowest in H+A, intermediate in L+A, and highest in L+B. Correspondingly, birds were more abundant, and nest density higher in areas with relatively more ground vegetation cover, higher vegetation structure (foliage density and cover), and greater heterogeneity (Chapter 2). To further document preference, I partitioned study plots into two groups as represented by their vegetation cover (cover and density); i.e. plots with low and high cover respectively. Based on nest densities, there was an apparent preference for high cover plots over those with low cover (Fig 1). This reflects the likelihood of birds choosing high over low cover habitat for nesting if the two habitat components are offered equally.

Adaptiveness and selection on preferences

To demonstrate that habitat preferences are adaptive, I examined whether fitness (nesting success) was higher in the preferred habitat. YBP and OTL entirely avoided highly grazed areas. Daily nesting success rate (a fitness component) of GP was lower ($Z = 2.5$, $P < 0.01$) under high grazing than low grazing. Highly significant differential mortality occurred between individuals that selected biennially and annually burned grasslands for nesting. Daily nesting success across species was higher ($Z = 2.4$, $P < 0.01$) in biennially than annually burned grasslands. Further, analysis of preference-performance relationships between birds nesting in the two cover habitat types showed that daily nesting success rate was significantly greater in preferred high cover habitats than at non-preferred low cover habitats (Fig 2, $\chi^2 > 4.3$, df = 1, $P < 0.05$ for all pairwise comparisons).

Natural selection on microhabitat choices

All three species showed strong positive selection differentials (s) and directional selection gradients (ß) more often than not for the critical habitat variables examined (Table 7). This was further supported by examination of the cubic spline curves (Figs 3a-d) for the respective critical vegetation variables that were considered. AC, YBP and OTL showed a negative selection for horizontal heterogeneity (Fig 3a, b and d, Table 7). In addition, OTL however also showed a negative selection for frequency of herbs (Fig 3b, Table 7).

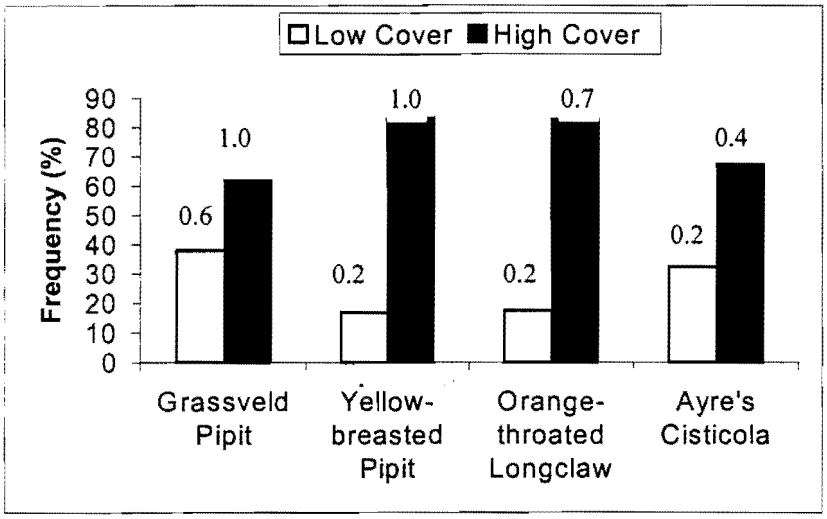

Fig 1. Frequency of nests placed in low and high cover habitats. The number above each pair of bars is the nest density per hectare.

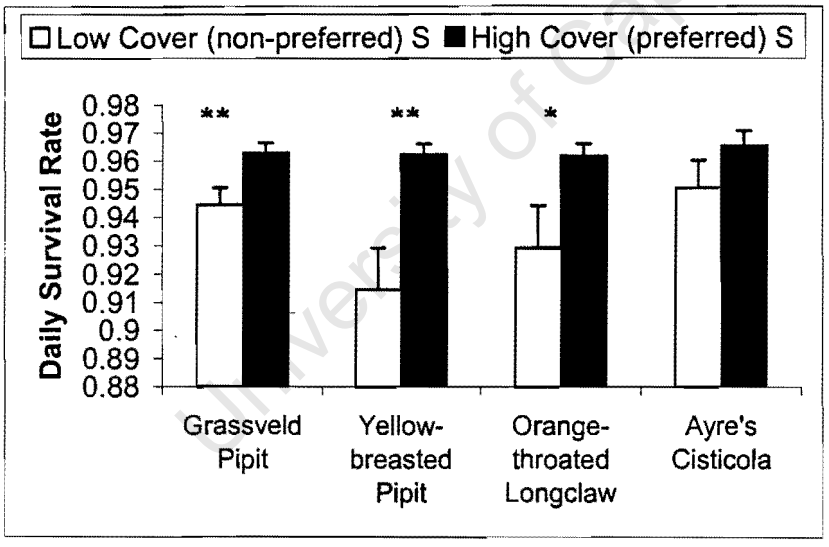

Fig 2. Daily survival rates (+1 SE) of nests in low cover (non-preferred) and high cover (preferred) habitat: Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Table 7. Standardized directional selection differentials (s) and selection gradients (ß) for vegetation characteristics associated with nesting survival. Data are means ± 1 SE. Asterisks indicate significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

vegetation	Grassveld Pipit		Yellow-breasted Pipit		Orange-throated Longclaw		Ayre's Cisticola	
	S	ß	*S*	ß	*S*	ß	*S*	ß
%GCOV					0.541 ± 0.187**	-0.675 ± 0.306**		
%HCOV					-1.345 ± 0.580**	-2.634 ± 0.846**		
MAXHGT	0.027 ± 0.004***	0.011 ± 0.006	0.027 ± 0.003***	-0.019 ± 0.005***				
HIT0-10	0.077 ± 0.012***	0.204 ± 0.051***			0.066 ± 0.012***	0.122 ± 0.043**	0.267 ± 0.060***	0.244 ± 0.075***
TOTHITS	0.013 ± 0.003***	-0.039 ± 0.011***			0.012 ± 0.002***	-0.013 ± 0.008		
CVTOTHITS							-1.109 ± 0.396***	-0.225 ± 0.454
CVMAXHGT			-1.431 ± 0.261***	-0.459 ± 0.315	-0.877 ± 0.230***	0.624 ± 0.289**		
HFD10								
VFD10	0.058 ± 0.020**	0.084 ± 0.028**	0.100 ± 0.022***	0.042 ± 0.022				

%GCOV = percentage grass cover; %HCOV = percentage herb cover; HIT0-10 = mean horizontal foliage density; TOTHITS = mean vertical foliage density; CVMAXHGT (coefficient of variation of the maximum height) = a measure of horizontal heterogeneity; CVTOTHITS (coefficient of variation of the mean total number of hits) = a measure of horizontal heterogeneity; HFD10 = horizontal foliage diversity; and VDF10 = vertical foliage diversity.

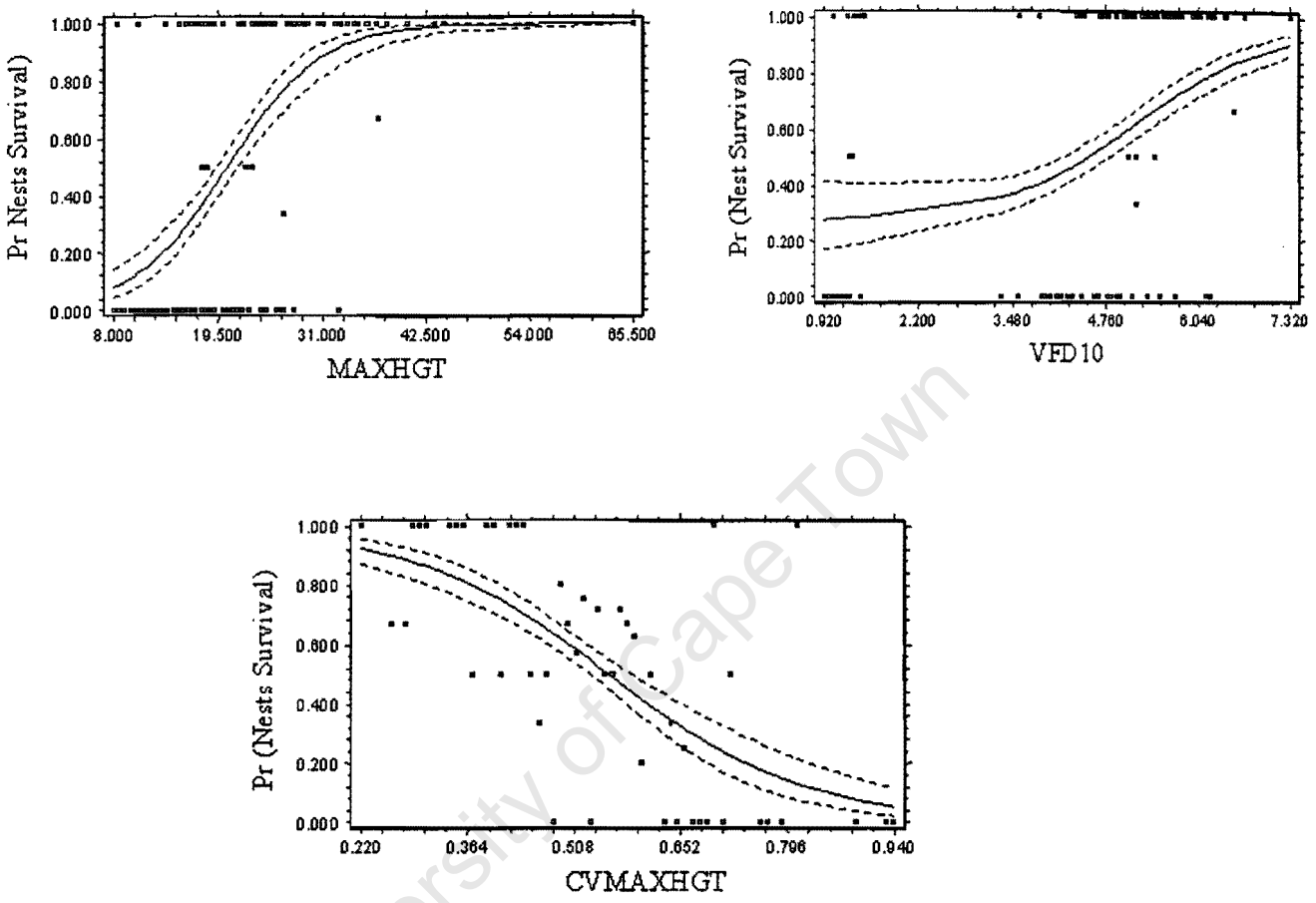

Fig 3a. Fitness surfaces (probability of nest survival) of Yellow-breasted Pipit as a function of the three critical vegetation features (MAXHGT – Mean maximum vegetation height, CVMAXHGT – Horizontal heterogeneity, VDF10 – Vertical foliage diversity) characterizing the bird species' nesting choice. Dashed curves indicate ± 1SE of predicted values from 200 bootstrap replicates of the fitness function.

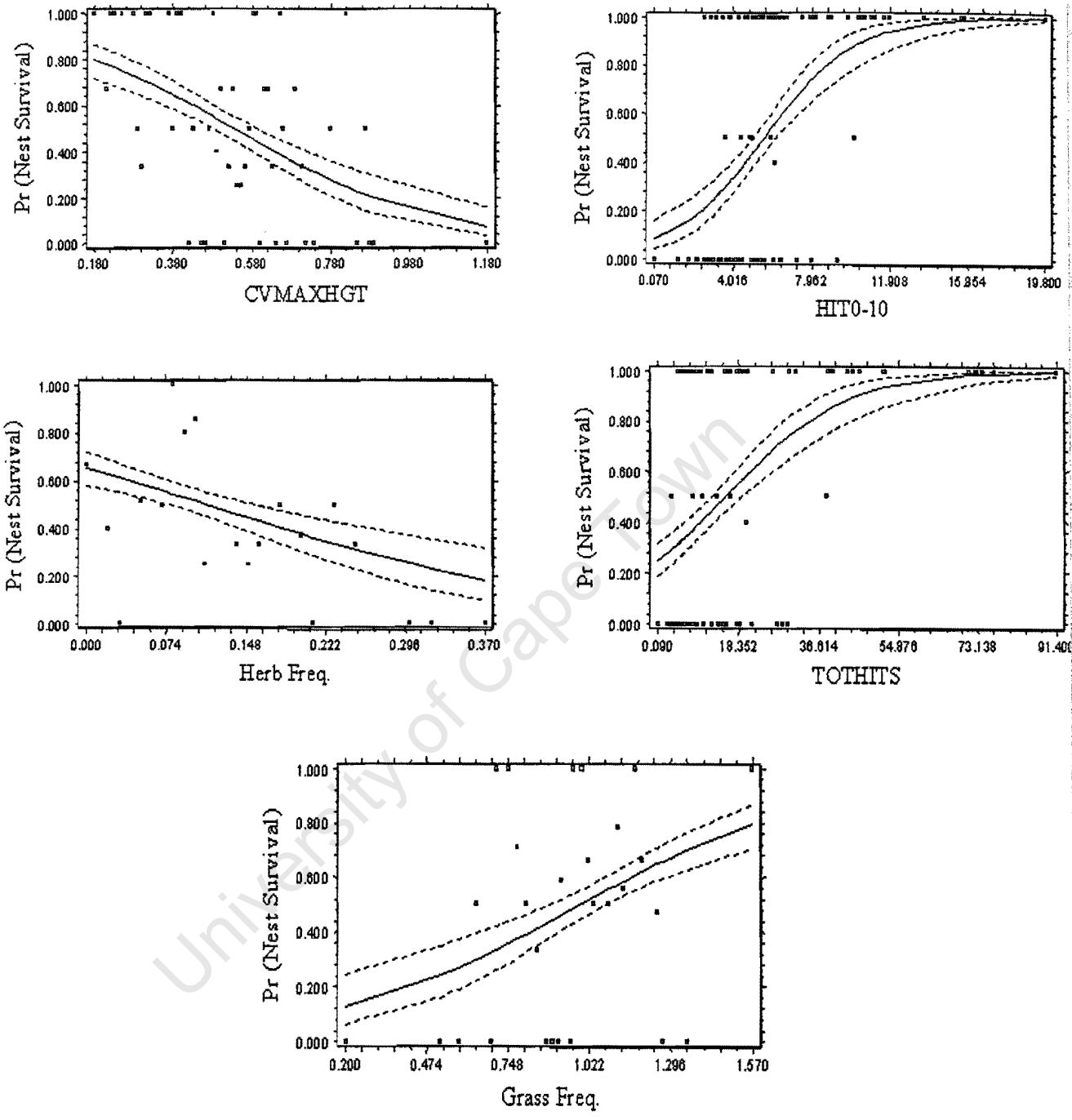

Fig 3b. Fitness surfaces (probability of nest survival) of Orange-throated Longclaw as a function of the six critical vegetation features (%GCOV – Percentage grass cover, %HCOV – Percentage herb cover, HIT0-10 – Mean horizontal foliage density, TOTHITS – Mean vertical foliage density, CVMAXHGT – Horizontal heterogeneity) characterizing the bird species' nesting choice. Dashed curves indicate ± 1SE of predicted values from 200 bootstrap replicates of the fitness function.

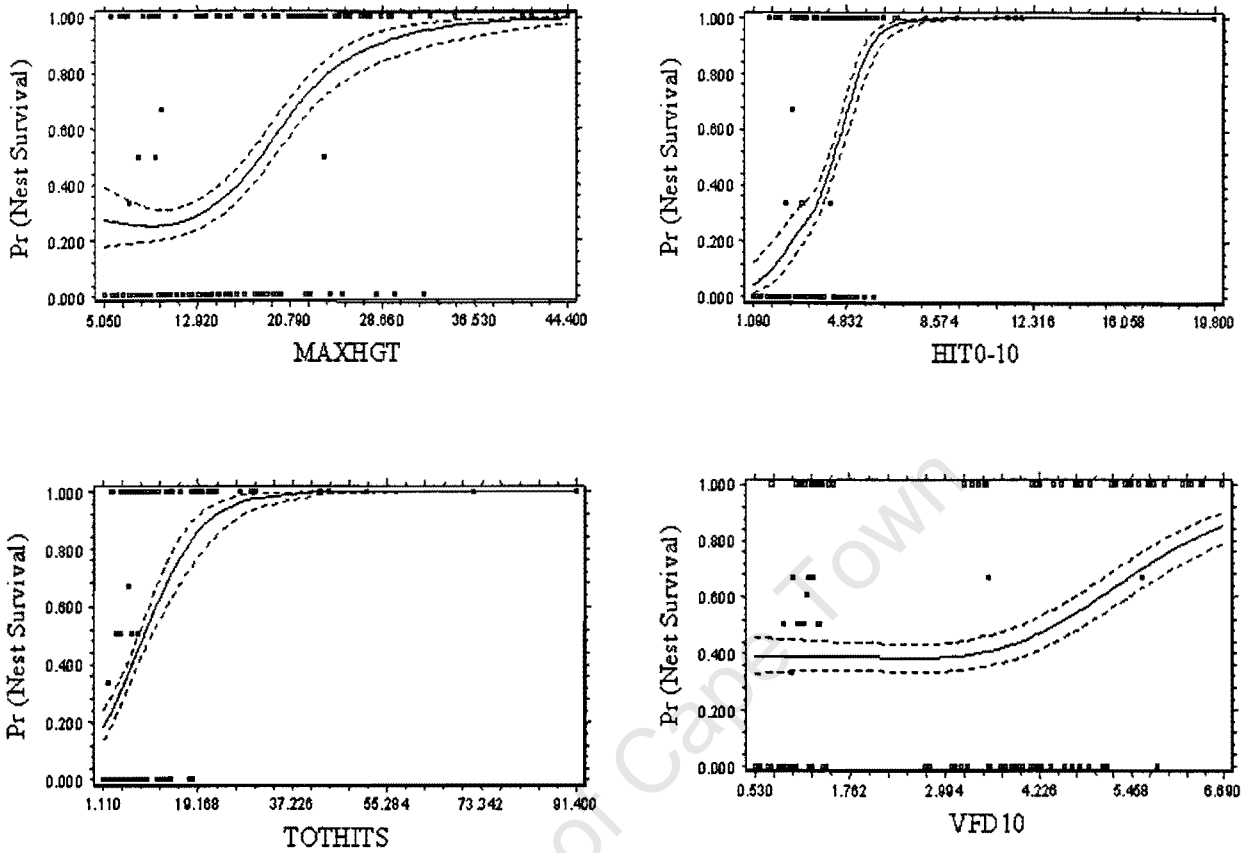

Fig 3c. Fitness surfaces (probability of nest survival) of Grassveld Pipit as a function of the four critical vegetation features (MAXHGT – Mean maximum vegetation height, HIT0-10 – Mean horizontal foliage density, TOTHITS – Mean vertical foliage density, VDF10 – Vertical foliage diversity) characterizing the bird species' nesting choice. Dashed curves indicate ± 1SE of predicted values from 200 bootstrap replicates of the fitness function.

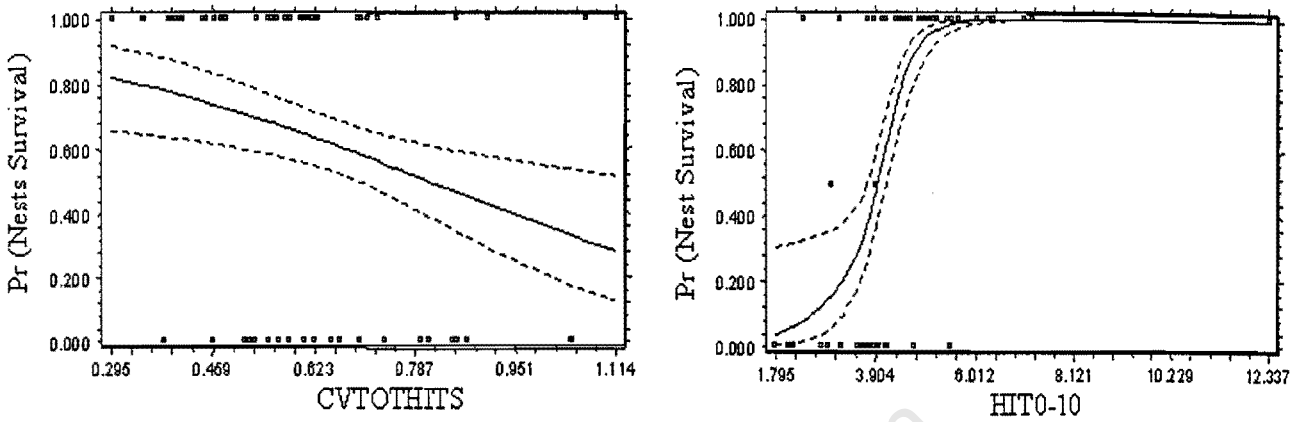

Fig 3d. Fitness surfaces (probability of nest survival) of Ayre's Cisticola as a function of the two critical vegetation features (HIT0-10 – Mean horizontal foliage density, CVTOTHITS – Horizontal heterogeneity) characterizing the bird species' nesting choice. Dashed curves indicate ± 1SE of predicted values from 200 bootstrap replicates of the fitness function.

DISCUSSION

Vegetation differences between nest sites and random sites

Nest sites differed from random sites for most of the habitat features of each of the four species indicating nonrandom nest-site selection. Other studies have demonstrated non-random selection of nest sites (e.g. see Martin and Roper 1988, Knopf and Sedgwick 1994, Badyaev 1995, Martin 1998). Low Wilk's lambda (for nest site vs. random) for AC (Wilk's lambda = 0.262), before any discriminant function was derived, indicated a high amount of discriminating power in the predictor variables suggesting that of the four species, they were most specific in their choice of nest sites. Of the three ecologically similar species, YBP was the most selective in choosing nest sites (YBP's Wilk's lambda = 0.335, OTL's Wilk's lambda =0.371, and GP's Wilk's lambda = 0.391).

Microhabitat differences between species

The nonrandom nest-site choices also differed between species. Correct classifications reflected general differences (or little overlap) between groups, while incorrect classification reflected similarities (or overlap). Differences in nest site can emerge from contrasting physiological endurance (e.g. see Martin 1998), adaptations among species, and competition among species for resources (nest sites), which may result in partitioning of nest sites. The high frequency of correct classifications suggested that birds were selecting specific habitat features in their nesting patches. GP chose nests sites with relatively open areas characterized with less ground vegetation cover, more herbaceous cover, lower vegetation structure (foliage density and cover) and lower heterogeneity compared to either OTL or YBP. The huge difference between AC and the other three species suggests that nest-site selection might be evolutionarily conservative. If selection of nest site is heritable, then selection should favour intraspecific differences in nest site selection to allow successful coexistence of species. Differential susceptibility to mortality by predation over evolutionary history between species may provide a possible explanation for the observed differences. That is, for species that may have historically suffered high nest predation risk, mortality caused by such high predation are thought to favour evolution of selection for seeking better cover (concealment) or selection for unusual nesting sites to reduce predation risk of nests. However, if predators do not search nests randomly, but can develop search images for patches associated with nests, then stereotypy in nest site placement should result in poor reproductive success (see Martin 1996a).

Incorrect classification reflected similarities in nest sites of the species suggesting that some birds are much less specialized and may often overlap with other species. Although OTL generally nest in areas with relatively greater vegetation cover, density, and vertical complexity, reduced availability of these features due to management disturbance (grazing and burning) may sometimes force them to place their nests in areas similar to either GP or YBP nesting sites. This may be the cause of the occasional misclassification in our analysis. Some birds may also place their nests in unusual places as this sometimes enhances nesting success (Filliater *et al.* 1994). Incorrect classification can also reflect behavioural responses to predation where birds change nest sites following a failed nesting attempt (e.g. see Martin 1992). Young birds might be forced to nest in non-preferred nest site due to competition. In addition, overlap in nest site may be a consequence of body condition of individuals. Inferior body condition of individuals may constrain the acquisition of preferred high quality nest sites forcing individuals with low body condition to nest in areas outside their normal preferred nest sites. The choice of nest site may therefore involve conflicting selection pressures. For example foraging, and nesting may require different habitats. Because incubation and caring for nestling are both energetically expensive activities requiring high-energy demands on adults (e.g. e.g. see Roff 1992), birds may trade off nesting sites with rich foraging sites by nesting in places unsuitable for nesting. Such a trade-off between predation (nesting sites) and food (foraging sites) may result in overlap (similarity) in nest sites between species. Overlap or similarity of nest sites may to incur fitness costs (e.g. nest predation) because the resulting increase in cumulative nest density can increase density-dependent predation rates (Martin 1988c, 1993c, 1996a).

Vegetation differences in relation to nesting success

Vegetation variables associated with successful nests differed from those associated with unsuccessful nesting attempts for all species. This suggests that choice of habitat features that influence the ability of birds to reproduce successfully should be favoured over evolutionary time. The total-foliage hypothesis (see Martin 1996a, 1993c) predicts that higher foliage density influences nesting success by concealing nests, inhibiting predator search, or hindering nest discovery through inhibiting transmission of chemical, visual and auditory cues (see Martin 1993). Selection for greater foliage cover may also be associated with the enhanced thermal environment of nest microhabitat (e.g. see Walsberg 1985,

Murphy 1993) leading to reduced likelihood of heat stress and cold stress, which enhance nest success. The fitness advantage gained by individuals using habitat features associated with successful nesting may have important consequences. Natural selection will eliminate offspring of birds choosing the 'wrong' nesting site features while potentially favouring the ability of organisms to identify and choose habitat features that define increased nesting success. However, this will only happen if habitat choice indeed has a genetic basis.

Identification of critical habitat features

Critical habitats are those that directly influence the ability of birds to reproduce successfully. Habitat variables that entered the model and which helped to distinguish nest sites from random sites, may not be the habitat features that are critical to fitness (also see Martin 1998). For example, although lower horizontal heterogeneity tended to be crucial for successful nesting, random sites had a higher horizontal heterogeneity than nest sites. Further, the difference suggests that, although greater structural heterogeneity might simultaneously provide high food resource and diversity of nesting substrates, the criteria for choice of nesting habitat may differ from that considered to meet other specific demands such as food, perch sites (see Matsuoka 1997). If selection gradients could favour and maintain selection for particular features through the process of natural selection, then habitat features that affect fitness could be more important in driving habitat selection. In particular, nest predation, the main cause of mortality in grassland birds (Chapter 2) may be the driving force that determines choice of nest sites (also see Martin and Roper 1988, Marzluff 1988). Thus, it may favour nests-site specialization and thus determine preferences for particular habitat features.

Adaptiveness and selection on preferences

Nest success was higher in preferred than non-preferred habitat for all the four species, indicating that preferences were adaptive. Natural selection can thus potentially favour the ability of birds to distinguish and identify habitat features influencing nest success. The strong positive directional selection coefficients and gradient selection for individual habitat features that determine fitness provide the basis for the evolution of nest site choices. It also suggests that these traits are under selection that can be maintained if selection has a genetic basis. Habitat choices are assumed to have a genetic basis (Jaenike and Holt 1991). Selection pressure will favour those individuals that succeed in their

nesting attempts. Thus, if the above assumption is true, then choice of habitat features that enhance reproductive success should be favoured over evolutionary time. Indeed, natural selection maintains features that enhance fitness (also see Jaenike and Holt 1991). Nest predation may favour nest site specialization to reduce overlap. However, in disturbed habitats, very strong positive selection for particular traits may be reduced by natural selection if individuals spend more time searching for them (which can amount to reduced individual fitness).

The negative standardized selection gradient for mean vertical foliage density (TOTHITS) indicated that vertical foliage density was not under selection when selections for other habitat features in the multivariate array were considered. Note that if a nest is well covered below 10 cm (HIT0-10; horizontal foliage density), any more cover on top (e.g. given by TOTHITS) may have no extra effect on enhancing fitness. A negative standardized selection gradient for vertical foliage density can also suggest that very thick vegetation was selected against. Such vegetation can reduce visibility of the approach of predators. Early detection of predators alerts the breeding bird and allows them to display cryptic and evasive behaviour. Use of herbs as nesting substrates was strongly selected against. Use of herbs as nesting substrates may have a bottle neck effect in the sense that rapid growth of the herbs may leave nests exposed for individuals nesting under herbs or choosing patch cover by herbs. The negative directional selection for horizontal heterogeneity reflects selection for individuals placing their nests in less uniform habitats. This might suggest that uniform distribution of vegetation interferes with the ability of predators to locate nests.

Univariate directional selection (*s*) differentials differed from the multivariate selection gradients (ß) in some cases suggesting that multiple (rather than single) habitat features were responsible for influencing fitness and nest site selection. The combinations of all positive multivariate selection gradients provided the major combination of critical traits for each species. Some traits (e.g. HIT0-10) appeared in the combination of traits enhancing nesting success across species suggesting that these were the major heritable determinants of nesting success.

Conclusion

This study clearly demonstrated that nest sites selection is non-random. The non-random nest site choice probably differs between species to allow coexistence of species because

overlap in nest site can incur substantial fitness cost. Although several factors are predicted to be selective forces that determines avian habitat selection (e.g. Holmes *et al.* 1986), this study suggests that nest predation risk can strongly influence nest-site selection. There is evidence that birds can respond to predation in their choice of nest sites (Martin 1996a, Sieving and Wilson 1998). Indeed, birds are known to choose breeding habitat based, in part, on risk of nest predation and actual nest predation events result in marked changes in re-nesting location (Greig-Smith 1982, Marzluff 1988), presumably to avoid subsequent attacks by the same predator (Morton *et al.* 1993). The fitness consequences of individuals differing in their selection for particular phenotypic traits suggest that preferences are adaptive. Estimation of fitness functions relating fitness of individuals to critical phenotypic traits (nest site) suggests that natural selection might be acting to favour preference for specific fitness-related habitat features. Taken together, my results add support to the idea that nest predation events can represent proximate and evolutionary mechanisms potentially influencing an individual's decision about where to nest (Martin 1998). The strong positive directional selection coefficients and gradient selection differentials for traits (nest site) that determine fitness provide the basis for evolution of nest site choices and suggest that these traits are under selection. Finally, this study identifies critical phenotypic traits (nest-site characteristics) that directly influence fitness. These are crucial for understanding the way in which organisms choose their habitats and for their conservation planning.

Appendix 1. Means (SD) of habitat characteristics between (A) nest site versus random site and (B) successful versus failed nests of four focal grassland bird species that nest in the Wakkerstroom high altitude grasslands and the univariate (ANOVA) of differences in the means.

		Yellow-breasted Pipit				Orange-throated Longclaw				Grassveld Pipit				Ayre's Cisticola			
(a)	Variable	Nest Site (150)	Random (54)	*F*	*P*	Nest Site (131)	Random (54)	*F*	*P*	Nest Site (170)	Random (54)	*F*	*P*	Nest Site (62)	Random (54)	*F*	*P*
	%GCOV	87.2 (23.9)	86.7 (12.0)	0.01	0.942	86.2 (22.9)	86.7 (12.0)	0.14	0.710	83.1 (20.5)	86.9 (12.0)	6.23	0.013	87.7 (20.2)	86.7 (12.9)	0.14	0.706
	%HCOV	7.9 (8.1)	10.3 (3.9)	4.36	0.034	9.3 (7.5)	10.3 (3.9)	0.89	0.347	9.6 (7.3)	10.3 (3.9)	0.44	0.507	10.0 (8.7)	10.3 (3.9)	0.03	0.862
	%TGCOV	96.1 (23.1)	97.4 (11.2)	2.49	0.116	96.9 (23.5)	97.3 (11.2)	0.48	0.488	94.3 (23.0)	97.4 (11.2)	11.83	0.001	97.3 (17.6)	97.3 (11.2)	0.00	0.971
	MAXHGT	23.37 (9.31)	18.10 (9.5)	12.57	0.001	25.56 (10.6)	18.1 (9.51)	20.24	0.001	16.77 (8.7)	18.1 (9.51)	0.91	0.341	20.29 (4.9)	18.10 (9.5)	2.44	0.121
	HIT0-10	5.89 (3.08)	3.52 (3.00)	28.14	0.001	6.54 (3.29)	3.52 (1.88)	40.01	0.001	4.47 (2.89)	3.52 (1.88)	5.09	0.025	4.81 (1.49)	3.52 (1.88)	17.14	0.001
	TOTHITS	18.27 (15.67)	5.63 (5.41)	33.58	0.001	19.40 (17.5)	5.63 (5.41)	32.23	0.001	10.9 (13.9)	5.63 (5.41)	7.34	0.007	7.72 (5.67)	5.63 (5.41)	4.09	0.046
	CVMAXHGT	0.52 (0.14)	0.57 (0.11)	5.06	0.026	0.51 (0.18)	0.57 (0.11)	6.29	0.013	0.63 (0.31)	0.57 (0.11)	1.60	0.207	0.55 (0.12)	0.57 (0.11)	1.55	0.215
	CVTOTHITS	0.52 (0.14)	0.82 (0.32)	88.21	0.001	0.54 (0.26)	0.82 (0.32)	39.56	0.001	0.67 (0.26)	0.82 (0.32)	12.23	0.001	0.61 (0.19)	0.82 (0.32)	18.49	0.001
	HFD10	5.77 (2.12)	2.07 (1.58)	137.25	0.001	5.28 (2.44)	2.07 (1.58)	79.72	0.001	6.34 (2.65)	2.07 (1.58)	126.4	0.001	4.91 (2.31)	2.07 (1.58)	58.13	0.001
	VFD10	4.36 (1.78)	1.33 (1.48)	124.37	0.001	3.91 (2.08)	1.33 (1.48)	68.33	0.001	3.00 (1.89)	1.33 (1.48)	35.09	0.001	1.80 (1.46)	1.33 (1.48)	2.89	0.092
(b)		Successful (83)	Failed (67)	*F*	*P*	Successful (69)	Failed (62)			Successful (81)	Failed (89)			Successful (39)	Failed (23)		
	%GCOV	89.1 (24.8)	83.0 (22.7)	8.33	0.005	88.8 (22.4)	83.0 (22.1)	8.38	0.005	85.2 (22.9)	81.3 (17.5)	5.57	0.019	88.2 (19.3)	85.2 (22.9)	1.42	0.238
	%HCOV	8.3 (8.2)	7.3 (8.00)	0.59	0.442	7.9 (5.9)	10.9 (8.7)	5.38	0.022	10.1 (8.6)	9.1 (6.0)	0.82	0.368	8.8 (8.4)	13.2 (10.2)	3.24	0.077
	%TGCOV	97.57 (20.7)	93.2 (25.7)	16.17	0.001	(21.5)	(24.8)	4.99	0.027	96.4 (23.3)	92.2 (21.3)	12.40	0.006	97.8 (18.6)	97.1 (16.2)	0.29	0.592
	MAXHGT	26.9 (9.2)	17.41 (6.3)	51.77	0.001	27.3 (9.87)	20.39 (7.4)	20.21	0.001	21.03 (9.4)	12.9 (5.76)	46.93	0.001	21.06 (4.5)	16.42 (5.4)	12.90	0.007
	HIT0-10	7.03 (3.41)	4.06 (1.52)	44.07	0.001	7.71 (3.79)	4.65 (1.20)	32.38	0.001	5.81 (3.59)	3.24 (1.09)	41.43	0.001	4.99 (1.55)	3.47 (0.89)	18.26	0.001
	TOTHITS	24.30 (17.91)	10.18 (7.5)	36.37	0.001	25.82 (20.8)	11.39 (8.8)	25.64	0.001	16.14 (18.53)	6.13 (3.41)	25.02	0.001	9.05 (6.66)	4.19 (1.37)	11.84	0.001
	CVMAXHGT	0.47 (0.12)	0.59 (0.14)	30.00	0.001	0.45 (0.17)	0.57 (0.18)	14.48	0.002	0.60 (0.42)	0.65 (0.16)	1.05	0.306	0.52 (0.14)	0.59 (0.09)	5.20	0.026
	CVTOTHITS	0.49 (0.14)	0.55 (0.14)	5.45	0.021	0.48 (0.19)	0.59 (0.32)	5.52	0.020	0.60 (0.20)	0.73 (0.29)	11.66	0.001	0.58 (0.19)	0.68 (0.18)	4.58	0.036
	HFD10	5.76 (2.16)	5.76 (2.01)	0.00	0.998	5.19 (2.18)	5.38 (2.73)	0.20	0.657	6.00 (2.68)	6.65 (2.60)	2.57	0.111	4.90 (2.66)	5.03 (1.61)	0.04	0.838
	VFD10	4.92 (1.63)	3.65 (1.72)	21.38	0.001	4.47 (1.99)	3.28 (2.02)	11.35	0.001	3.44 (2.09)	2.60 (1.61)	8.60	0.004	2.20 (1.69)	1.09 (0.21)	9.82	0.003

5

Concealment is the key to nest survival in grassland bird communities

Abstract

I examined the relationship between nest-site and nest-patch characteristics, and nest predation risk in three ecologically similar ground-nesting grassland bird species, the Yellow-breasted Pipit *Hemimacronyx chloris*, Grassveld Pipit *Anthus cinamomerous*, and Orange-throated Longclaw *Macrony capensis*, which breed in the Wakkerstroom high altitude grassland, South Africa. The likelihood of nest predation clearly depended upon habitat structure (foliage) at the immediate vicinity of the nest as well as the vegetation surrounding the nest at the scale as large or larger than the nest patch. In general, variables that are important in discriminating between successful and depredated nests across all species were directly related to vegetation cover, density and horizontal heterogeneity. Successful nests across all species were placed in denser foliage with thicker cover than depredated nests. Mean horizontal vegetation heterogeneity at the nest patch tended to be higher for depredated nests across species, suggesting that the uniform distribution of the vegetation interfered with the ability of predators to locate nests. My results emphasize the need to consider both nest-site characteristics and nest-patch characteristics in studies of nest predation.

INTRODUCTION

Nest predation is the major factor influencing reproductive success for many passerine birds (Ricklefs 1969, Martin and Roper 1988, Chapter 2) and is thought to be a critical factor shaping many aspects of avian behaviour (Skutch 1949, Lindern and Møller 1989, Kuleza 1990, Martin and Li 1992, Bosque and Bosque 1995, Martin 1996b). Few studies have examined factors affecting risk of predation in birds. The variability in nest site placement can directly affect the fitness of individuals using them (see Martin 1998, Stokes and Boersma 1998). Consequently, birds should place their nests in microhabitats that reduce the risk of predation (see Martin 1988b, Chapter 4).

Nest survival may be affected by microhabitat at two spatial scales (Martin and Roper 1988): (1) nest site (characteristics within the immediate vicinity of the nest) and (2)

nest patch (characteristics of the habitat patch surrounding the nest). Increased nest concealment in the immediate vicinity of the nest (nest site) will reduce the probability of nest predation – "nest concealment hypothesis." Increases in vegetation density and complex vegetation at a scale as large or larger than the nest patch will also reduce the probability of nest predation – "the total-foliage hypothesis" (Martin 1993c). The two hypotheses are not mutually exclusive; rather their negative effects on fitness are additive. The nest site hypothesis has been supported by some studies (e.g. Martin and Roper 1988, Murphy 1983, Kelly 1993, Norment 1993), while others have not (Best and Stuffer 1980, Holway 1991, Howlett and Stutchbury 1997). Studies in aquatic systems have shown that foliage density at the scale as large or larger than the nest patch often reduces predation risk (e.g. see Crowder and Cooper 1982). Yet, only few studies of birds have attempted to relate vegetation characteristics at the scale of nest patch to nest predation risk.

In this paper, I examine the relationship between nest-site and nest-patch characteristics and nest predation risk in three ground-nesting grassland bird species in the high altitude grassland, South Africa. I addressed losses of nests to predators only; losses due to other causes of mortality are not considered here.

STUDY AREA AND METHOD

The study was conducted in the high altitude grasslands of Wakkerstroom in Mpumalanga province, South Africa at 1800-2200 m a.s.l. from 1998-2001. The study area (centered at 27° 10' S, 30° 06' E) is located on the high lying grassveld between 1800m to 2250m elevations. Wakkerstroom's main vegetation types with respect to altitude and soil type, as classified by Low and Rebelo (1996), are Moist Sandy Highveld Grassland dominated by *Themeda triandra*, *Digitaria thicholaenoides*, *Tristachya leucothrix* and *Hetropogon contortus*; North-eastern Mountain Grassland which is dominated by *Tristachya leucothrix, Loudetia simplex and Diheteropogon filifolius*; Moist Clay Highveld Grassland dominated by *Themeda triandra* and Natal Central bushveld dominated. The main land use in the Wakkerstroom district is large-scale livestock farming. These grasslands are managed in three ways, viz. heavily grazed and annually burned (H+A), lightly grazed and annually burned (L+A), and lightly grazed and biennially burned (L+B). Vegetation varies considerably between management regimes. In particular, vegetation varies with respect to floristic characteristics, vegetation cover, density, and structural heterogeneity.

Three ecologically similar species of ground-nesting grassland birds of the family Motacillidae were selected for this study, viz. Yellow-breasted Pipit *Hemimacronyx chloris* (YBP), Grassveld Pipit *Anthus cinamomerous* (GP), and Orange-throated Longclaw *Macrony capensis* (OTL). All three species are commonly multiple brooded and they build a new nest in a different location at each nesting attempt.

Nest searches and monitoring

The whole study area was intensively searched for nests throughout the study period from 1998 to 2001. Searching and locating of nests was done by dragging a 50m rope between two observers to flush out birds from nests, or based on behavioral observation. Nests were visited at 1-5 day intervals to record their status until the nesting process was completed or had been terminated. Nests were considered successful if one or more young fledged. Conversely, if all nest contents (i.e. eggs or nestling) disappeared simultaneously, the nest was considered to have been depredated.

Vegetation sampling

Nest-site and nest patch characteristics were measured following techniques modified from Wiens and Rotenberry (1981). Nest-site and nest-patch vegetation characteristics were measured at nests only after completion or termination of nesting. All these data were collected within 2 weeks after the nesting episode. At each nest I measured eight nest-site variables and 10 nest-patch variables. Vegetation variables at nest sites were measured at 10-cm intervals along 100-cm transects extending outwards from the nest in the four cardinal directions. The nest patch was considered to be the vegetation > 1 m < 10 m from the nest. Vegetation features at the nest patch were measured at 1m intervals along a 10m tape extending outwards from the nests in each of the four cardinal directions. At each sampling point for both nest site and nest patch, a thin (6-mm diameter) rod was placed vertically through the vegetation to the ground, and the number of contacts ("hits") with plants within 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm and 50-100 cm heights intervals recorded. The plant species making contact with the rod at each 10-cm interval of the tape was also recorded. Bare ground or presence of rocks was noted when vegetation or litter was absent at the point of contact with the ground. The following eight nest site variables were then recorded. (1) Height of the primary concealing vegetation (NSCHGT). (2) Percentage grass cover at nest site (%NSGCOV). (3) Percentage herb

cover at nest site (%NSHCOV). The percentage coverage of grasses and herbs was calculated as the frequency of occurrence of each type at all 44 samples along transects. (4) Percentage total ground cover at nest site (%NSTGCOV), calculated as the proportion of all points not recording bare ground or rocks. (5) Mean vegetation height at nest site (NSHGT), given by the maximum height of the rod recording contacts with vegetation. (6) Mean horizontal foliage density at nest site (NSHIT0-10), calculated as the number of contacts of vegetation with the rod in the 0-10 cm height intervals. (7) Mean vertical foliage density at nest site (NSTOTHIT), calculated as the mean total number of contacts over the entire height of the rod. (8) Nest detectability (DETEC). Nest detectability at each nest was measured by estimating the amount of lateral cover afforded nests in each of the four cardinal directions and from above. This was estimated as the percentage of a 5x5 cm fluorescent orange card marker attached to the nest that was visible from a distance of 1 m away from the nest sides and 1 m directly above the nest roof. Similarly, the following 10 variables were also recorded. (1) Percentage grass cover at nest patch (%NPGCOV). (2) Percentage herb cover at nest patch (%NPHCOV). (3) Percentage total ground cover at nest patch (%NPTGCOV). (4) Mean vegetation height at nest patch (NPHGT). (5) Mean horizontal foliage density at nest patch (NPHIT0-10). (6) Mean vertical foliage density at nest patch (NPTOTHIT). (7) Horizontal heterogeneity, calculated using the coefficient of variation of the maximum height interval with hits (CVHGT). (8) Horizontal heterogeneity, calculated using the coefficient of variation of the mean total number of contacts over the entire height of the rod. (9) Horizontal foliage diversity (HFD10), calculated using a heterogeneity index according to Wiens and Rotenberry (1981). (10) Vertical foliage diversity (VDF10), calculated using the Shannon diversity index.

DATA ANALYSIS

I used both uni- and multivariate methods to test for differences in the vegetation characteristics between successful and depredated nests for each bird species. Univariate comparisons involved 1-way ANOVA (Sokal and Rohlf (1995). Variables that discriminated between successful and depredated nests were identified by stepwise discriminant function analysis (SDFA). This analysis helped to further investigate relationships between nest-site and nest-patch characteristics, and nest predation. All 18 variables were included in this analysis. Equality of the covariance matrices was tested using Box's *M* criterion. For each pair of groups tested, the covariance matrices were un-

equal (P<0.05). Discriminant function analysis was then based on the pooled within-group covalence matrix, where Wilks' lambda was used to determine the combination of variables providing the best group separation, and using Mahalonobis distance (Minimum D^2) between group centroids as the criterion for maximizing separation of groups (Hand 1981, Williams 1983). Moderate violations of equality of the covariance matrices probably have little effect on two-group classification success and *F*-tests can still be powerful (Cooley and Lohnes 1971, Williams 1983). Finally, original variables selected by SDFA were correlated with the discriminant function to examine their importance. Group sample sizes differed. Thus, the classification performance of each SDFA was tested against a chance model using Cohen's Kappa and its associated Z-value (Titus *et al.* 1984).

I performed all the statistical analyses using STATISTICA software (StatSoft Inc, 2000). Significance levels for statistical tests were set at $P < 0.05$. Percentage data were arcsine transformed to more closely fit the normal distribution. Means are presented ± standard deviation (SD).

RESULTS

Vegetation differences between successful and depredated nest

The mean values of most nest-site variables and nest-patch variables differed significantly between successful and depredated nests for all species (Table 1-3). In all species, depredated nests were placed in vegetation characterised with lower nest concealment, lower foliage density, lower ground vegetation cover, lower vertical heterogeneity, and greater horizontal heterogeneity than for successful nests. Discriminant function analysis further emphasised the importance of both nest-site and nest-patch characteristics in influencing nest predation for all species (Table 4-6). In all analyses, the number of correctly classified cases indicated that nest fate was strongly dependent on specific features (Table 4-6). For YBP, successful and depredated nests were discriminated significantly (Wilk's lambda = 0.463, Minimum $D^2 = 4.9$, $P < 0.0001$; approx. $F = 44.4$, df = 3, 115) using three of the 18 variables considered (DETEC, CVHGT, %NSHCOV). Briefly, successful YBP nests were distinguished from depredated nests by having a combination of lower detectability at the nest site (DETEC) (i.e. greater nest concealment), lower nest patch horizontal heterogeneity (CVHGT), and fewer herbs at the nest site (%NSHCOV) (Table 4). Four of the 18 variables considered discriminated between successful and depredated OTL nests (NPHIT0-10, DETEC, %NPTGCOV, CVGHT)

(Wilk's lambda = 0.541, Minimum $D^2 = 3.4$, $P < 0.0001$; approx. $F = 17.2$, df = 4, 81). Briefly, successful OTL nests had greater horizontal foliage density at nest patch (NPHIT0-10), lower detectability at nest site (DETEC) (i.e. greater nest concealment), higher ground cover at nest patch (%NPTGCOV), and lower nest patch horizontal heterogeneity (CVHGT) than depredated nests. A model that included six out of the 18 variables significantly discriminated between successful and depredated GP nests (DETEC, NSHIT0-10, %NPTGCOV, NSCHGT, NSHGT, NSTOTHIT) (Wilk's lambda = 0.404, Minimum $D^2 = 5.9$, $P < 0.0001$; approx. $F = 20.6$, df = 6, 84). Successful GP nests tended to be placed in vegetation with lower detectability (DETEC) (i.e. greater nest concealment), greater horizontal foliage density at the nest site (NSHIT0-10), greater ground cover at the nest patch (%NPTGCOV), taller primary concealing vegetation (NSCHGT), greater mean vegetation height at nest site (NSHGT) and greater mean vertical foliage density at nest site (NSTOTHIT), than for depredated nests.

Table 1. Means (±SD) of nest-site and nest-patch characteristics of successful and depredated Yellow-breasted Pipit nests and the univariate (ANOVA) of differences in the means. Where appropriate, data were arcsine transformed before statistical analysis.

Variables	Depredated	Successful	*F*	P
		Nest site		
DETEC (%)	0.448 (18.4)	15.4 (13.7)	112.0	0.0001
NSCHGT	23.71 (8.90)	33.98 (9.86)	33.7	0.0001
%NSGCOV	84.0 (25.5)	92.1 (25.6)	13.0	0.0004
%NSHCOV	4.7 (5.4)	6.8 (8.0)	2.4	0.1238
%NSTGCOV	91.9 (26.4)	98.8 (19.1)	35.8	0.0001
NSHGT	17.84 (7.41)	27.85 (8.13)	47.1	0.0001
NSHIT0-10	4.76 (2.34)	8.09 (3.74)	29.8	0.0001
NSTOTHIT	14.85 (9.73)	29.32 (16.27)	30.3	0.0001
		Nest patch		
%NPGCOV	82.9 (23.3)	89.4 (26.2)	7.5	0.0072
%NPHCOV	5.8 (5.2)	8.1 (8.7)	2.6	0.1097
%NPTGCOV	91.8 (24.9)	97.5 (21.2)	18.1	0.0001
NPHGT	16.29 (6.78)	27.25 (9.58)	46.8	0.0001
NPHIT0-10	4.05 (1.74)	7.33 (3.54)	34.8	0.0001
NPTOTHIT	12.08 (8.03)	27.21 (17.57)	30.8	0.0001
HFD10	6.77 (1.91)	6.19 (2.00)	2.5	0.1171
VFD10	4.63 (0.78)	5.53 (0.71)	43.3	0.0001
CVHGT	0.60 (0.16)	0.46 (0.13)	28.3	0.0001
CVTOTHIT	0.55 (0.15)	0.49 (0.15)	4.7	0.0329

Table 2. Means (±SD) of nest-site and nest-patch characteristics of successful and depredated Orange-throated Longclaw nests and the univariate (ANOVA) of differences in the means. Where appropriate, data were arcsine transformed before statistical analysis.

Variables	Depredated	Successful	*F*	*p*
		Nest site		
DETEC	0.384 (0.201)	15.4 (17.4)	34.7	0.0001
NSCHGT	30.19 (9.60)	37.55 (11.81)	10.2	0.0020
%NSGCOV	87.7 (27.6)	95.2 (22.8)	11.9	0.0009
%NSHCOV	5.0 (4.6)	4.7 (5.5)	0.1	0.7757
%NSTGCOV	96.0 (26.3)	99.6 (17.5)	16.6	0.0001
NSHGT	24.02 (8.37)	33.97 (10.83)	23.1	0.0001
NSHIT0-10	5.98 (2.92)	11.30 (5.22)	34.5	0.0001
NSTOTHIT	20.11 (10.57)	45.50 (26.89)	33.9	0.0001
		Patch site		
%NPGCOV	83.1 (24.6)	90.4 (25.4)	7.5	0.0077
%NPHCOV	8.6 (7.4)	7.7 (6.2)	0.3	0.5590
%NPTGCOV	95.2 (28.8)	98.3 (22.5)	4.9	0.0289
NPHGT	20.02 (7.18)	31.21 (9.44)	38.8	0.0001
NPHIT0-10	5.16 (2.03)	9.61 (3.71)	48.5	0.0001
NPTOTHIT	15.82 (7.89)	37.11 (19.56)	44.7	0.0001
HFD10	6.17 (2.74)	5.62 (2.15)	1.1	0.2953
VFD10	4.95 (0.73)	5.74 (0.66)	28.1	0.0001
CVHGT	0.56 (0.21)	0.40 (0.16)	17.5	0.0001
CVTOTHIT	0.50 (0.23)	0.46 (0.19)	0.9	0.3472

Table 3. Means (±SD) of nest-site and nest-patch characteristics of successful and depredated Grassveld Pipit nests and the univariate (ANOVA) of differences in the means. Where appropriate, data were arcsine transformed before statistical analysis.

Variables	Depredated	Successful	*F*	*P*
		Nest site		
DETECT	53.2 (25.0)	16.6 (14.1)	82.7	0.0001
NSCHGT	20.67 (11.11)	26.43 (9.42)	7.2	0.0087
%NSGCOV	77.6 (20.8)	88.1 (29.1)	13.1	0.0005
%NSHCOV	6.5 (8.2)	0.050 (0.071)	0.9	0.3533
%NSTGCOV	88.2 (21.8)	95.4 (25.4)	13.7	0.0004
NSHGT	13.80 (5.95)	22.60 (10.11)	27.4	0.0001
NSHIT0-10	3.58 (0.97)	8.10 (5.03)	39.5	0.0001
NSTOTHIT	10.00 (3.92)	28.38 (21.72)	35.2	0.0001
		Nest patch		
%NPGCOV	79.3 (20.2)	86.6 (26.6)	7.3	0.0082
%NPHCOV	7.1 (5.5)	8.1 (7.9)	0.5	0.4789
%NPTGVCOV	89.5 (22.8)	96.2 (27.2)	12.6	0.0006
NPHGT	12.10 (5.29)	26.86 (34.29)	9.2	0.0031
NPHIT0-10	3.27 (1.03)	7.03 (4.56)	32.8	0.0001
NPTOTHIT	8.49 (3.47)	25.06 (22.11)	27.9	0.0001
HFD10	7.83 (2.51)	7.67 (2.45)	0.1	0.7649
VFD10	4.15 (0.73)	5.14 (1.01)	30.0	0.0001
CVHGT	0.65 (0.15)	0.66 (0.56)	0.0	0.9453
CVTOTHIT	0.65 (0.22)	0.63 (0.22)	0.3	0.5651

Table 4. Means (±SD) of habitat characteristics that are important in discriminating between successful and depredated nests of Yellow-breasted Pipits, Univariate (ANOVA) of differences in the means and results of stepwise discriminant function analysis are given. Variables are given in the order in which they were entered in the model.

Univariate analysis					Discriminant analysis			
Variable	Successful (75)	Depredated (45)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	*P*
DETEC (%)	0.448 (18.4)	15.4 (13.7)	112.0	0.0001	0.802	-0.891	-0.898	0.0001
CVHGT	0.60 (0.16)	0.46 (0.13)	28.3	0.0001	0.501	-0.440	-0.373	0.0030
%NSHCOV	4.7 (5.4)	6.8 (8.0)	2.4	0.1238	0.482	0.132	0.268	0.0358
						Eigenvalue	1.157	
Correctly classified	88.0%	74.5%						
Z = 6.6***								

Table 5. Means (±SD) of habitat characteristics that are important in discriminating between successful and depredated nests of Orange-throated Longclaws, Univariate (ANOVA) of differences in the means and results of stepwise discriminant function analysis are given. Variables are given in the order in which they were entered in the model.

	Univariate analysis				Discriminant analysis			
Variables	Successful (n = 43)	depredated (43)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	*P*
NPTOTHIT	15.82 (7.89)	37.11 (19.56)	44.7	0.0001	0.618	0.816	0.654	0.0011
DETEC	0.384 (0.201)	15.4 (17.4)	34.7	0.0001	0.600	-0.696	-0.530	0.0039
%NPTGCOV	95.2 (28.8)	98.3 (22.5)	4.9	0.0289	0.580	0.263	-.0499	0.0187
CVHGT	0.56 (0.21)	0.40 (0.16)	17.5	0.0001	0.576	-0.515	-0.443	0.0252
						Eigenvalue	0.848	
Correctly classified Z = 6.3***	83.7%	83.7%						

Table 6. Means (±SD) of habitat characteristics that are important in discriminating between successful vs. depredated nests of Grassveld Pipits, Univariate (ANOVA) of differences in the means and results of stepwise discriminant function analysis are given. Variables are given in the order in which they were entered in the model.

	Univariate analysis				Discriminant analysis			
Variables	Successful (43)	Depredated (51)	*F*	*P*	Wilk's lambda	Structure coefficient	Standard coefficient	*P*
DETECT	53.2 (25.0)	16.6 (14.1)	82.7	0.0001	0.629	-0.805	-0.877	0.0001
NSHIT0-10	3.58 (0.97)	8.10 (5.03)	39.5	0.0001	0.415	0.535	1.071	0.1364
%NPTGVCOV	89.5 (22.8)	96.2 (27.2)	12.6	0.0006	0.412	0.313	0.194	0.2036
NSCHGT	20.67 (11.11)	26.43 (9.42)	7.2	0.0087	0.448	0.247	-0.805	0.0035
NSHGT	13.80 (5.95)	22.60 (10.11)	27.4	0.0001	0.443	0.449	1.009	0.0058
NSTOTHIT	10.00 (3.92)	28.38 (21.72)	35.2	0.0001	0.414	0.507	-1.171	0.1551
						Eigenvalue	1.474	
Correctly classified	81.4%	92.2%						
Z = 7.1***								

DISCUSSION

The likelihood of nest predation clearly depends upon the vegetation characteristics in the immediate vicinity of the nest as well as the vegetation surrounding the nest at the scale as large or larger than the nest patch. This emphasizes the need to consider both nest-site and nest-patch characteristics in studies of nest predation (e.g. see Martin and Roper 1988, Norment 1993). In general, variables that are important in discriminating between successful and depredated nests across all species were directly related to vegetation cover, density and horizontal heterogeneity. Successful nests across all species were placed in denser foliage with thicker cover than depredated nests. Mean horizontal vegetation heterogeneity (the magnitude of spatial variation in vegetation) tended to be higher for depredated nests across species, suggesting that more uniform distribution of the vegetation interfered with the ability of predators to locate nests.

Nest concealment hypothesis: nest-site effects

Poorly concealed nests were more likely to be depredated than well concealed nests, suggesting that most predators find nests by actively searching for them. Detectability index (or degree of concealment) entered into all models discriminating between successful and depredated nests and pointed to the universal importance of nest concealment at the immediate vicinity of the nest in reducing predation risk. Increased nest concealment would be expected to reduce predation risk from diurnal predators that use visual cues to locate nests. Suricates *Suricata suricatta* and Yellow Mongoose *Cynictis penicillata* which are common in our study, are diurnal and rely on sight to find nests. Other visual oriented predators that I observed in my study area include birds like Fiscal Shrike *Lanius collaris*, Stanley's Bustard *Neotis denhami*, and Red-chested Sparrow Hawk *Accipiter rufiventris* and snakes like Rinkhals *Hemachatus haemachatus*, Rhombic Skaapsteker, *Psammophylax rhombeatus*, Brown House Snake *Lamprophis fuliginosu*, and Short-snouted Grass Snake *Psammophis brevirostris* among others. Thus, increased concealment may decrease the ability of these predators to locate nests. The importance of nest concealment by foliage in reducing the probability of nest predation has been demonstrated in other studies (e.g. Keppie and Herzog 1978, Westmoreland and Best 1985, Martin and Roper 1988; but see Best and Stauffer 1980).

Total-foliage hypothesis: nest-patch effects

Characteristics of the surrounding vegetation within 10 m of the nest had a clear effect on the probability of nest survival with dense foliage in the nest patch reducing nest predation. Greater foliage density in the nest patch may impede both random and intentional nest discovery by concealing nests, inhibiting predator search, or hindering nest discovery through inhibiting transmission of chemical, visual and auditory cues. Dense and homogenous vegetation surrounding the nest may reduce predation rates of the nests by providing increased number of potential nest sites to be searched which reduces nest detection by predators actively searching the vegetation for nests (e.g., see Martin 1988c, Martin and Roper 1988, Knopf and Sedgwick 1992). This in turn reduces predator search efficiency by increasing the time and effort of searches. Low horizontal heterogeneity of habitat neighbouring the nest may also prevent common predators from developing search images for nests. Dense foliage at the nest patch can reduce risk of predation by concealing parental movement and activity from predators. This can result in reduced nest detectability and vulnerability to predation by predators that use parental movements to locate nests. Dense and complex vegetation in the nest patch may thus reduce predator search efficiency even for poorly concealed nests. of bird nests that rely on visual cues to detect. In addition, predators themselves may avoid habitats with thick vegetation altogether to avoid been eaten by their own predators. The support of the hypothesis that total foliage density (total vegetation) in the nest patch influences predation probability has also been documented in both terrestrial (e.g. see Bowman and Harris 1980, Martin and Roper 1988, Norment 1993) and aquatic systems (see Crowder and Cooper 1982). Taken together, my results add support to the idea that although ignored in most studies of nest predation, habitat patch characteristics may be as important as nest site characteristics in influencing fitness, and both need to be considered in nest-predation studies.

Although the nest concealment hypothesis and the total foliage hypothesis are taken as two separate hypotheses, the two are not mutually exclusive; rather their negative effects on fitness are additive. They should be viewed as a single hypothesis because they both test the effect of the degree of nest concealment on predation risk and they do not make any mutually exclusive predictions regarding the outcomes of breeding events. Because nest disturbance associated with our visit to nests does not affect predation risk I am confident in believing that variables under examination affected nest predation rates of grassland birds (see Appended Chapter A).

In conclusion, this study suggests that nest-site selection at both nest-site and nest-patch scales have consequences for individual fitness. Although several factors can potentially act as selective forces in shaping avian habitat preferences (e.g. Holmes *et al.* 1986), nest predation risk can strongly influence nest-site selection (Greig-Smith 1980, Marzluff 1988, Morton *et al.* 1993, Martin 1996a, Sieving and Wilson 1998). Traditionally, habitat has been thought to influence nest survival only at the fine scale of the nest site and nest sites are accordingly considered to be abundant (Ricklefs 1969, Lack 1971). Now that data are available to suggest that habitat parameters also affect fitness at a broader scale, high-quality nest sites may not be as abundant as traditionally presumed (Martin and Roper 1988).

6

The role of fire frequency in influencing patterns of parental care, nestling growth and body condition of grassland birds

Abstract

I obtained an index of food abundance and conducted field experiments to compare food provisioning, nestling growth, body condition, nest attentiveness and time spent brooding at two management-mediated grassland habitat types. The two grassland types, which differed in their burning frequency, were lightly grazed and annually burned and lightly grazed and biennially burned. Three ecologically similar grassland species of the family Motacillidae bred on the study area: Yellow-breasted Pipit *Hemimacronyx chloris*, Grassveld Pipit *Anthus cinamomerous*, and Orange-throated Longclaw *Macrony capensis*. Although food abundance differed significantly between the two management habitat types, my study yielded no evidence for an effect of management-mediated food abundance on feeding rate, nestling provisioning rates, nestling growth rates, body condition, nest attentiveness or time spent brooding. This suggested that food availability alone may not be the most important factor influencing the production of offspring.

INTRODUCTION

Availability of food is often considered to be the most important factor influencing the production of offspring and variation in life history traits of birds (Lack 1968, Roff 1992, Martin 1987; but see Ricklefs 1969, Martin 1995a). Nestling growth and survival are particularly sensitive to variation in food supply in several bird species (e.g. Perrins 1965, von Bromssen and Jansson 1980, Prince and Ricketts 1981, Quinney 1982, Ricklefs *et al.* 1984, Holthuijzen 1990, Magrath 1990, Wiggins 1990, Rondenhouse and Holmes 1992).

Low food availability can considerably constrain the amount of food delivered to nestlings (e.g. see Harris 1969, Quinney 1982). Increases in parental food provisioning rates can cause increases in nestling growth and body condition. Thus, we might expect growth and body condition of nestlings raised in sites where food is most abundant to be superior to those raised in sites where food is less abundant. If parents increase foraging effort to compensate for the low food supply then they are expected to impair their own

health, especially among small passerines that cannot store much body fat (Garnet 1981). Reproduction is energetically expensive and may deplete the reserves of the parent (Roff 1992). Parent birds nesting and rearing young in areas of low food availability can also thus be expected to be of poorer body condition than those nesting and rearing young at sites where food is more abundant. As incubation places high energy demands on adults (Ruiz *et al.* 2000), the quality of foraging areas in the vicinity of the nests should be important during the incubation period as well. Indeed, food supply can influence schedules of parental care (Weathers and Sullivan 1989). If food is abundant, parent may forage for shorter periods and spend more time attending to the nest (nest attentiveness and brooding).

In this paper, I first test whether food abundance varies in relation to fire frequency. Second, I test whether differences in food abundance affect: (a) food provisioning rates, (b) nest attentiveness, (c) time spent brooding, (d) nestling growth rates and (e) nestling and adult body condition. I present data for three ground-nesting grassland bird species, the Yellow-breasted Pipit *Hemimacronyx chloris*, Grassveld Pipit *Anthus cinamomerous*, and Orange-throated Longclaw *Macrony capensis*, which breed in the high altitude grasslands of Wakkerstroom, South Africa.

METHODS

The study was conducted in the high altitude grasslands of Wakkerstroom (centred at 27° 10' S, 30° 06' E), Mpumalanga province, South Africa during the summers of 1998 to 2001. Six study plots were laid out in each of the two management systems, viz. lightly grazed and annually burned (L+A) and lightly grazed and biennially burned (L+B). These plots were separated from adjacent ones by at least 500m wide strips and measured approximately 25 ha each in size. Vegetation differences were measured for each grassland habitat type following techniques modified from Wiens and Rotenburry (1981) (See chapter 2 for details). Nests were searched over three breeding seasons from 1998 to 2001. Searching and locating of nests was done by rope dragging to flush birds out from their nests, or based on behavioural observation. Rainfall data were recorded from five rain gauges spread widely over the study area. All areas received equal amounts of rain.

Measurements of arthropod abundance (food availability)

Arthropods were sampled along three transects (each 500 m long) located at 100m, 250m and 400m from the edge of each study plot fence and running perpendicular to each plot fence. Monthly arthropod abundance was estimated over the entire breeding season (October to April the following year) from 1998 to 2001. Using sweep nets, 600 sweeps per plot (200 at each of the three transects) were done during each monthly food survey. Sweep nets have been shown to be superior to other sampling techniques in terms of measuring overall arthropod abundance in grasslands and are efficient in catching most of the prey groups eaten by the Motacillidae (Brodmann and Reyer 1999).

Food provisioning and parental care

Video cameras were used to record food provisioning patterns (number and size of food item brought and food delivery to nest), nest attentiveness and brooding by parents. Birds were video-taped during their incubation and nestling stages in 2001. Sony camcorders with 360x Digital zoom lenses were set up on tripods as low as possible at a distance of 3 – 5 m from nests. All camcorders were placed in a well camouflaged hide. During the incubation stage, video recording were made on any day after the confirmed day of clutch completion. During the nestling period, all video recordings were made when the nestling were 9-10 days old, or one or two days after primary feathers broke their sheaths. No nests were sampled more than once per nesting stage. Video recording was restricted to nests containing a clutch or brood size of three, this being the mean and modal size for all three species in my study area. Each videotaping season lasted six hours beginning at 07h00 and ending at 13h00. From each videotape, I recorded the frequency of feeding trips to the nest by both parents and where possible the number, size and type (order) of food item delivered during each feeding trip. Prey size was determined by comparing the length of the prey item (or the prey load when there was more than one item that could not be distinguished) with the size of the parent's bill (mean bill length = 17 mm for GP and YBP, 21 mm for OTL). I also scored the volume of prey items by comparing the volume of the item to the volume of the parent's bill, using five classes: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, and 4 bill-equivalents. Provisioning rate was expressed as total bill-equivalents of food received per hour. From each videotape, I also measured the time that parents spent incubating eggs and brooding nestling, as well as the number of off bouts (time away from the nest) per hour. Duration of attentiveness (incubation) and brooding during each visit were

determined by subtracting departure time from arrival time for each incubating or brooding visit respectively. The number of feeding trips to the nest by both parents per hour, prey mass delivered per hour, nest attentiveness per hour and brooding time per hour were averaged over the six hours for each nest. This was then averaged across nests in order to obtain mean values for each species. At least six video samples (mean = 11 nests per species during incubation, and 23 nests per species during the nestling stage) were collected per species (Yellow-breasted Pipit, Orange-throated Longclaw, and Grassveld Pipit) in each of the two grassland management systems (i.e. L+A and L+B). A total of 203 nests were sampled in this way.

Measurements of nestling growth rates and body condition

Measurements of weight and tarsus length were taken every second day after hatching, up to the tenth day of the 14-day nestling period (day of hatch = day 0). I did not take measurements after day 10, as nestlings may fledge prematurely if handled after that age. Nestlings were individually marked (with a tiny mark) on different parts of the body (tarsus, belly and tibia) with a non-toxic marker. All nestlings were weighed during the morning hours using a 60-g Pesola spring balance (accuracy of 0.1 gram). The length of the right tarsus was measured by a single observer from the full joint to the bent toes with a sliding calliper to the nearest 0.1 mm. Potential differences in nestling growth in relation to fire frequency were assessed by comparing the mean body mass of nestlings at Day eight, and overall growth rate across species. To estimate growth curves, I fitted logistic curves to the mass data of day 0 to day 10 as described by Ricklefs (1967). From these curves, the rate of gain in nestling body mass between day 2 and day 10 was calculated according to Ricklefs (1967). This included the time to grow from 10% to 90% of asymptotic mass (maximum mass).

Nestling mass and tarsus length was used to measure nestling body condition at Day eight using the residual body mass according to Hochachka and Smith (1991). Body mass and structural size measurements (tarsus and wing length) were taken for 110 adults. Residuals from a Model I regression of body mass on tarsus length (and wing length for adults) were used as an index of condition (Ots *et al.* 1998).

DATA ANALYSIS

Data for both the number of feeding trips per hour, load sizes and food volume delivered per hour were normalised by square root transformation. All within-year comparisons were conducted using Mann-Whitney *U* tests using one-tailed probabilities at the 0.05 level of significance. Differences in parental feeding rates, load sizes, provisioning rates, nest attentiveness and time spent brooding in grassland under varying fire frequencies were tested using a paired *t*-test across the three species. Intraspecific comparisons of nestling mass and tarsus length at eight days of age were made using a paired *t*-test (Sokal and Rolf 1995).

RESULTS

A range of arthropods were collected in the sweep nets, viz. Coleoptera (beetles), Diptera (fry), Saltatoria (grasshopper and crickets), Hymenoptera (wasps and bees), Heteroptera, Menoptera (ants), Odonata (dragonflies), Arachnida (spiders) and Lepidoptera (caterpillar larvae). Relative food abundance in both fire regimes treatments were similar among years (Mann-Whitney *U* test, $P > 0.05$ in both cases). Consequently, data were pooled during subsequent analyses. Mean arthropod abundance was significantly greater under annual (33.9 ± 19.8 g) than under biennial burning (16.9 ± 9.6 g) (Mann-Whitney *U* test, $U = 441.5$, df = 86, $P < 0.0001$) (Figure 1). The study species are fairly generalised in their diet on the breeding ground, based on the wide variety of arthropods taken during normal foraging (Keith *et al.* 1992) and collar samples of nestling and video monitoring on food provisioning (this Chapter). All arthropods sampled were included in the food abundance estimates.

Food delivery rates did not vary in relation to fire frequency (7.04 ± 0.13 hr^{-1} versus 6.30 ± 0.24 hr^{-1}, Paired *t*-test, $P > 0.05$) (Fig. 2). Similarly, there were no differences in mean provisioning rate $hour^{-1}$ (volume of food delivered hr^{-1}) between annually and biennially burned grasslands (15.17 ± 0.04 bill-equivalents hr^{-1} versus 13.66 ± 0.37 bill-equivalents hr^{-1}, Paired *t*-test, $P > 0.05$) (Fig. 3).

Mean nestling mass at 8 days of age did not vary with fire frequency for all three species (25.0 ± 8.9 g versus 23.7 ± 6.9 g) (Paired *t*-test, $P > 0.05$). The rate of gain in nestlings body mass between day 2 and day 10, which included the time to grow from 10%

to 90% of asymptotic mass (maximum mass), similarly did not vary with fire frequency (Fig. 4-6).

There were no differences in both adult and nestling body condition between annually and biennially burned grasslands across all three species (mean weight = 30.4 g, tarsus length = 31.0 mm, wing length = 88.4 mm, residual = 0.00, versus mean weight = 33.0 g, tarsus length = 32.7 mm, wing length = 91.8 mm, residual = 0.00, Paired *t*-test, $P > 0.05$).

The number of trips from the nest per hour during incubation period, the mean time spent incubating the eggs per hour, and mean time spent brooding the nestling per hour did not vary in relation to fire frequency either (Paired *t*-test, $P > 0.05$ in all cases). This was the case for all three species in question (Fig. 7-9).

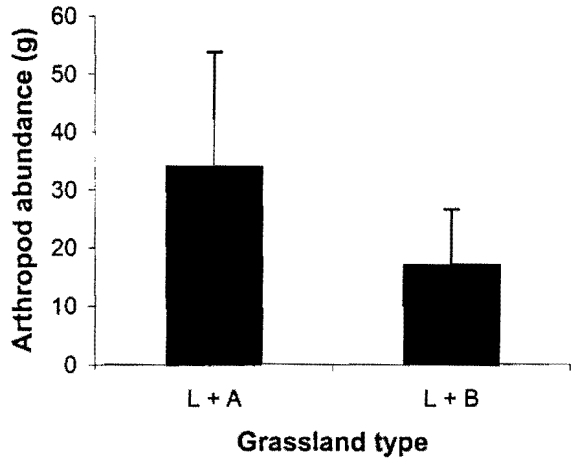

Figure 1. Mean (± SD) arthropod abundance in lightly grazed and annually burned (L+A) and lightly grazed and biennially burned (L+B) grasslands. During each breeding season from 1998 through 2001, 600 sweeps were made monthly with a sweep net in each of the six 500 m^2 study plots. Mean arthropod food abundance was significantly greater in L+A grassland than in L+B grassland (Mann-Whitney U test, $U = 441.5$, df = 86, $P < 0.0001$).

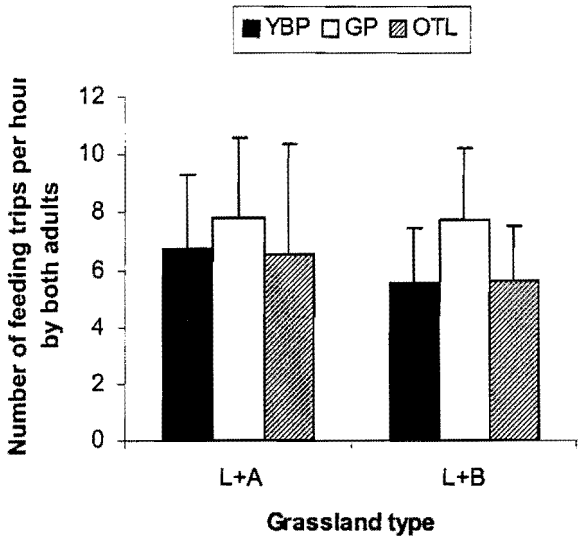

Figure 2. Rate at which parents deliver food to their nestlings (trips hr^{-1} ± SD) in lightly grazed versus annually burned (L+A) and lightly grazed and biennially burned (L+B) grasslands. There was no significant difference in feeding rates between the two grassland types within and across species. Species: GP, Grassveld Pipit; YBP, Yellow-breasted Pipit; OTL, Orange-throated Longclaw. (Paired *t*-test, $P > 0.05$).

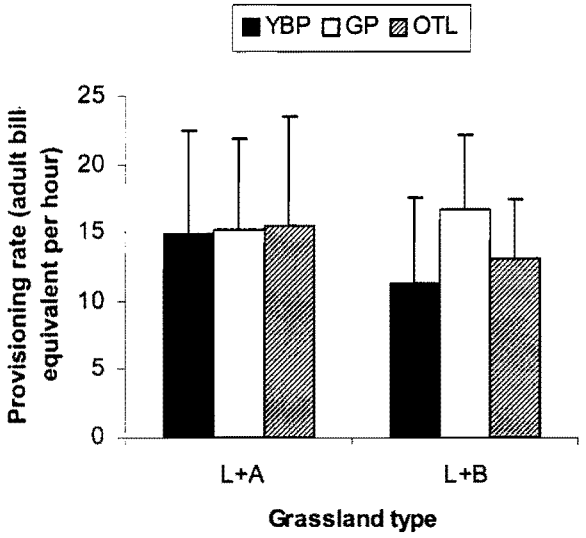

Figure 3. Provisioning rates (volume of food measured as adult bill-equivalents hr-1 ± SD) by parents to their nestlings in lightly grazed and annually burned (L+A) versus lightly grazed and biennially burned (L+B) grasslands. There was no significant difference in provisioning rates between the two management systems within and across species. Species: GP, Grassveld Pipit; YBP, Yellow-breasted Pipit; OTL, Orange-throated Longclaw. (Paired *t*-test, $P > 0.05$). (Paired *t*-test, $P > 0.05$).

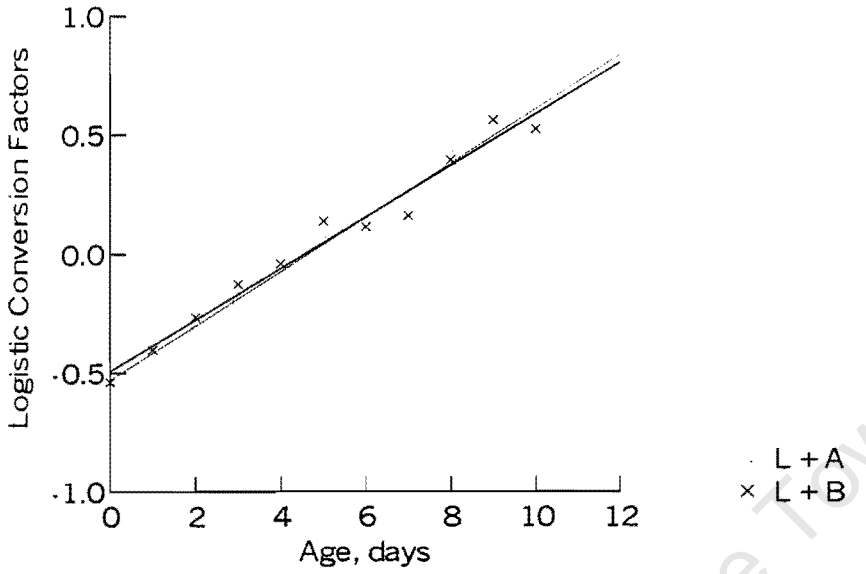

Figure 4. Converted growth curves of the Yellow-breasted pipit in annually (L+A) versus biennially burned (L+B) grassland. The rate of gain (slope of the two lines) in nestling body mass between Day 2 and Day 10, which included the time to grow from 10% to 90% of asymptotic mass (maximum mass) were not significantly different between L+A (slope = 0.1129/day, K = 0.452) and L+B (slope = 0.1048/day, K = 0.419) management systems. Ricklefs 1967 graphical method.

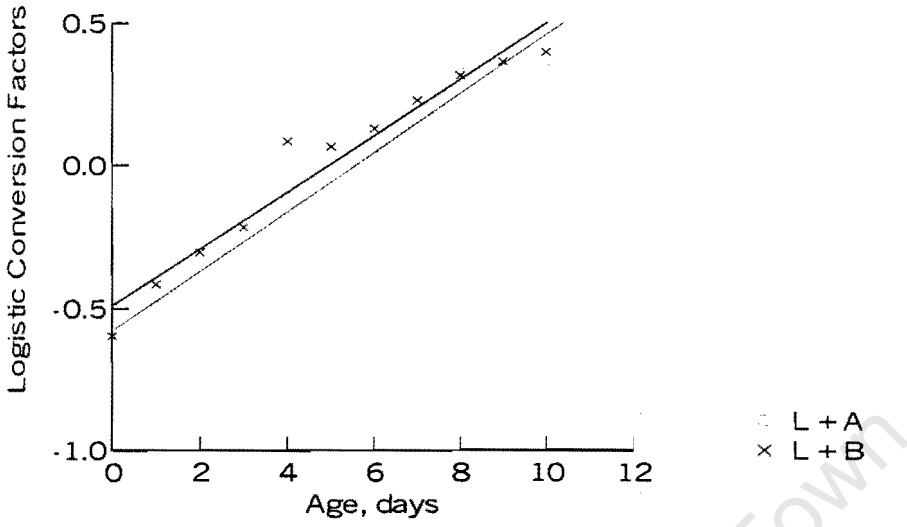

Figure 5. Converted growth curves of the Grassveld Pipit in annually (L+A) versus biennially burned (L+B) grassland. The rate of gain (slope of the two curves) in nestling body mass between Day 2 and Day 10, which included the time to grow from 10% to 90% of asymptotic mass (maximum mass) were not significantly different between L+A (slope = 0.1250/day, K = 0.500) and L+B (slope = 0.1210/day, K = 0.484) management systems. Ricklefs 1967 graphical method.

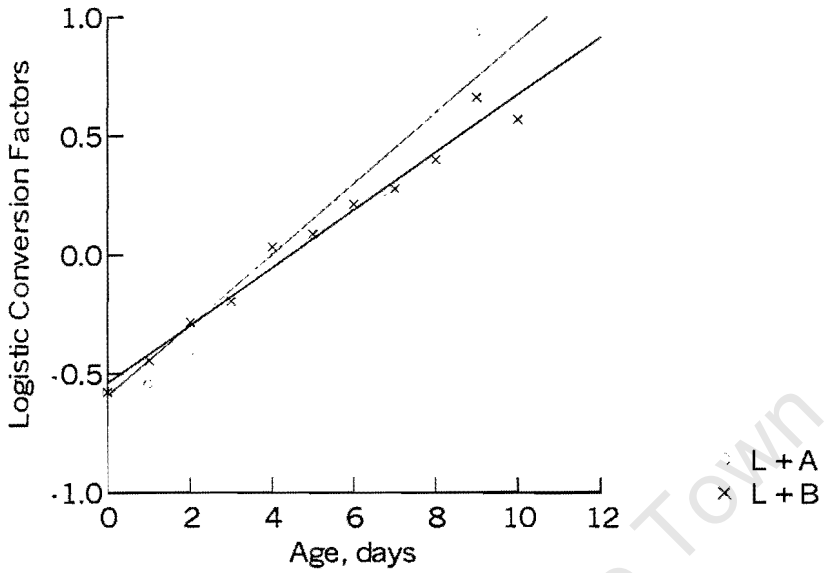

Figure 6. Converted growth curves of the Orange-throated Longclaw in annually (L+A) versus biennially burned (L+B) grassland. The rate of gain (slope of the two curves) in nestling body mass between Day 2 and Day 10, which included the time to grow from 10% to 90% of asymptotic mass (maximum mass) were not significantly different between L+A (slope = 0.1472/day, K = 0.589) and L+B (slope = 0.1210/day, K = 0.484) management systems. Ricklefs 1967 graphical method.

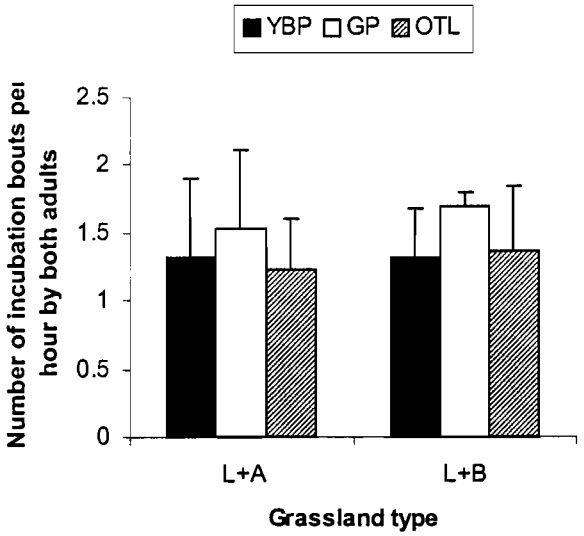

Figure 7. Number of incubation bouts by both adults (trips hr^{-1} ± SD) in lightly grazed versus annually burned (L+A) and lightly grazed and biennially burned (L+B) grasslands. There was no significant difference in number of in bouts between the two grassland types within and across species. Species: GP, Grassveld Pipit; YBP, Yellow-breasted Pipit; OTL, Orange-throated Longclaw. (Paired *t*-test, $P > 0.05$).

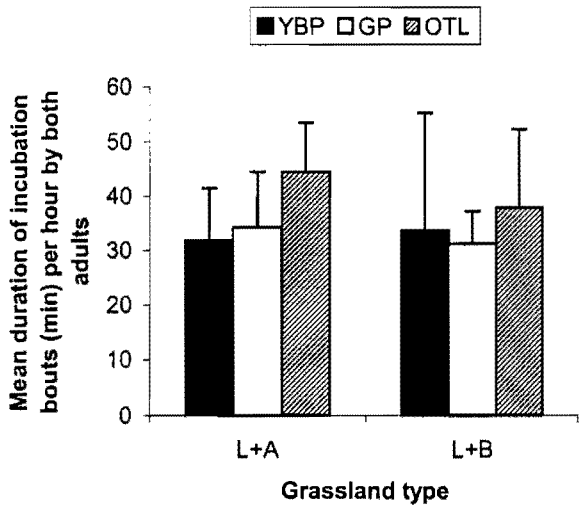

Figure 8. Mean duration of incubation bouts by both adults (min hr^{-1} ± SD) in lightly grazed and annually burned (L+A) versus lightly grazed and biennially burned (L+B) grasslands. There was no significant difference in mean duration of incubation bouts between the two grassland types within and across species. Species: GP, Grassveld Pipit; YBP, Yellow-breasted Pipit; OTL, Orange-throated Longclaw. (Paired *t*-test, $P > 0.05$).

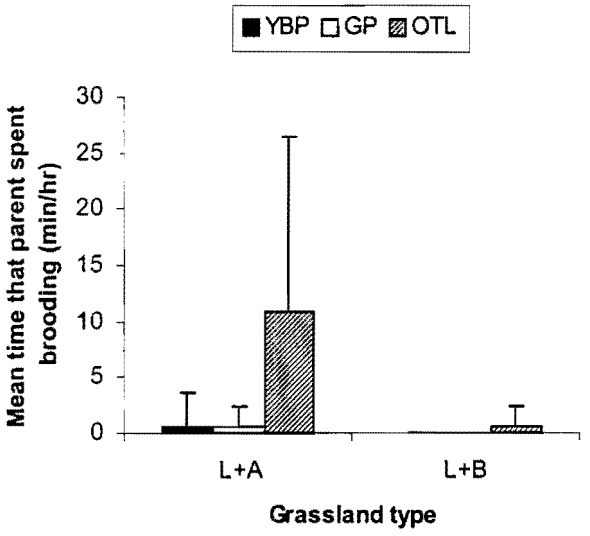

Figure 9. Mean time spent brooding nestlings by parent birds (min hr^{-1} ± SD) in lightly grazed and annually burned (L+A) versus lightly grazed and biennially burned (L+B) grasslands. There was no difference in mean brooding time between the two management systems within and across species. Species: GP, Grassveld Pipit; YBP, Yellow-breasted Pipit; OTL, Orange-throated Longclaw. (Paired *t*-test, $P > 0.05$).

DISCUSSION

Relative abundance of prey

Both vegetation characteristics (density, cover and heterogeneity) and abundance of arthropod food available to breeding birds differed between annually burned and biennially burned grasslands, suggesting that vegetation characteristics can index food availability (also see Martin 1988b). The study species appear to be fairly generalised in diet on the breeding ground, based on the wide variety of arthropods taken during normal foraging (Keith *et al.* 1992) and collar samples of nestling and video monitoring on food provisioning. Based on video images of food brought to nestlings and collar samples of nestling, there was excellent correspondence between the taxa or arthropods collected in the sweep nets and those delivered by parents to their nestlings. Thus, all arthropod sampled were justifiably considered to be potential prey.

Food provisioning, nestling growth rates and body condition between grassland types

Prey density is typically believed to positively affect foraging success of grassland birds (Brodmann *et al.* 1977), and thus food delivery rates to nestling. Feeding conditions of nestlings during the growth stage have been shown to have a significant effect on both the growth and final size attained (Ricklefs and Peters 1981). Although food abundance was significantly higher in annually burnt compared to biennially burnt grasslands, this study yielded no evidence for an effect of food abundance on feeding rates, provisioning rates, or nestling growth. These results may be explained in several ways. First, prey density may not affect feeding conditions of nestlings and/or targeted growth (e.g. see Wiggins 1990), suggesting that growth rate and body size are heritable (e.g. see Schluter and Smith 1986). Alternatively, parents do not feed their nestlings with more than the required amount of food. Second, nestlings in grassland with low food resources may be able to compensate for poor feeding condition through higher food conversion efficiency or other compensatory mechanisms. Adults may have adjusted their feeding behaviour with respect to choice of food provided to nestlings. For example, although nestlings in both grassland types were mainly fed with grasshoppers, caterpillars (larval arthropods), prey was delivered at a relatively higher frequency in annually than biennially burned grasslands. Caterpillars may be more accessible in biennially burned grasslands. Although compensatory growth in wild birds is still poorly understood, studies of growth in domestic chickens have shown that under laboratory conditions, birds may compensate for periods of

under-nutrition by accelerating growth at a later stage (Wilson Osbourn 1960). Third, parents nesting in biennially burned grasslands may be of higher quality in terms of body condition and parenting performance than those nesting in annually burned grassland. Such parents would be able to effectively search and provide nestlings with enough food even when food is scarce, and to utilise their body reserves thus masking any possible deterioration of their condition. Birds might have better concealment under biennial burning (Chapter 5). Thus, although food may be scarcer in biennially burned grasslands, they might be better concealed from predators. However, if parents increase foraging distance to compensate for scarcity of food, long distances to feeding areas would, however, increase the risk of nest predation as nests are left unattended for longer periods of time. Other studies have also failed to detect effects of food availability on food provisioning and growth rates (e.g. Omland 1994, Wiggins 1990).

Nest attentiveness and brooding

The lack of an overall difference in mean time spent incubating and brooding between annually burned and biennially burned grasslands suggest that the duration of incubation bouts and time spent brooding are not sensitive to food abundance.

Conclusion

Food availability alone may not be the major evolutionary driver of life history variation among bird species suggesting the need to consider other possible alternatives such as nest predation. Indeed, management practice-mediated reproductive dysfunction via nest predation could be a more important factor than food availability in influencing for example provisioning rates (by constraining the rate at which parent birds visit nests to feed their young), which in turn can influence growth and health state of the nestling and life history traits such as clutch size. In addition, higher nest predation rates are associated with a shorter nesting cycle (Martin 1995a), and thus higher nestling growth rates.

7

Nest predation of grassland bird species increases with parental activity at nest

Abstract

Alexander Skutch predicted that nest predation will increase with activity at nests, and that predation should be greatest during the nestling stage when parents are feeding young. I tested this hypothesis using three ecologically similar grassland bird species nesting on the high altitude grasslands of Wakkerstroom, South Africa. Parental activity, measured as adult arrival and departure frequency from the nest, was greater during the nestling than incubation stage. Nest predation, however, did not increase with parental activity between these stages in all three study species. However, nest-site effects could have confounded this result. I therefore conducted an experiment that controlled for parental activity (by reusing natural nests of the study species with artificial clutches) in order to test for nest-site effects. Nests that had a high risk of predation when used by active parents had a correspondingly high risk of depredation when the same nests were reused with artificial clutches (i.e. after controlling for parental activity). This result supports the notion that variation in nest-site quality is the primary factor affecting nest predation risk. I also tested whether high predation during incubation is related to nest-site effects. Nest predation rates of experimental clutches placed in nests that were depredated during incubation when active parents were present were significantly higher than those depredated during the nestling stage when active parents were present. However, once nest-site effects were accounted for, nest predation showed a positive increase with parental activity during the nestling stage both within and across species.

INTRODUCTION

Nest predation is the main cause of nest failure in many passerine birds (Ricklefs 1969, Lima, 1987, Martin and Clobert 1996, Chapter 2). Despite the fact that clutch size is one of the traits showing close adjustments to local conditions (Lack 1968), the proximate underlying mechanism by which clutch size is adjusted remains poorly understood. The evolution of clutch size has long been attributed to food (Lack 1948, Charnov and Krebs 1974) or to nest predation (Slagsvold 1982, Martin 1995a, Julliard *et al.* 1997, Martin *et al.*

2000a). Skutch (1949) hypothesized that increased parental activity can proximately increase the risk of nest predation which constrains the rate at which parent birds can deliver food to young. This in turn constrains clutch size through the limited number of young that parents can feed. Skutch's hypothesis predicts that if activity at nests is positively correlated with risk of predation, then nest predation should be higher during times of greater activity. This hypothesis and the positive proximate response has only received partial support (e.g. see Martin *et al.* 2000b; but see Roper and Goldstein 1997). Although there is some evidence that species at higher risk of nest predation show lower parental activity (Martin 1996b, Martin and Ghalambor 1999, Conway and Martin 2000), this hypothesis has not been tested widely. However, in order to test this hypothesis, one must first show the positive proximate relationship between parental activity and nest predation.

Nest-site effects may confound the relative importance of parental activity in influencing nest predation rates. Birds may also modify their behaviour to compensate for the risk of nest predation caused by nest-site effects (Møller 1989, Cresswell 1997). Three alternatives are possible: (1) parental presence and activity have no effect and nest-site characteristics influences nest predation risk; (2) nest sites have no effect and parental presence and activity influences nest predation; and (3) nest-site characteristics, parental presence and activity balance each other in influencing nest predation so that there will be no observable change in the risk of predation with variation in activity between stages.

In this chapter, I test these alternatives using three ecologically similar species breeding in Wakkerstroom high altitude grasslands, South Africa. First, I investigate whether predation rates generally increase with activity between stages by comparing parental activity and nest predation rates during the incubation and nestling stages. Second, I conduct an experiment that excludes parental activity in order to isolate nest-site effects. Finally, I examine whether predation increases proximately with parental activity once nest site effects are removed.

STUDY AREA AND METHODS

The study was conducted in the high altitude grasslands of Wakkerstroom, South Africa at 1800-2200 m a.s.l. from 1998-2001. Here grasslands are managed in three different ways, viz. heavily grazed and annually burned (H+A), lightly grazed and annually burned (L+A), and lightly grazed and biennially burned (L+B). Vegetation varies considerably across

management regimes with respect to floristics, vegetation cover, density, and structural heterogeneity (Chapter 3). Most birds did not breed in patches that were both heavily grazed and annually burned.

I examined parental activity and nest predation rates for three ecologically similar grassland species of the family Motacillidae breeding in the study area: Yellow-breasted Pipit *Hemimacronyx chloris* (YBP), Grassveld Pipit *Anthus cinamomerous* (GP), and Orange-throated Longclaw *Macrony capensis* (OTL).

Nests were located in three consecutive breeding seasons between 1998 and 2001. Searching and locating of nests was done by dragging a 50m rope between two people to flush out birds from nests, or based on behavioural observation. Nests were marked (for relocation) with a stick or stone placed 10 m away from each nest. Nests were visited at one to five days (1-5day) intervals to determine the nest fate (successful or failed) until the nesting process terminated. A serious effort was made to minimize disturbance of breeding birds and their nests. To this end, gloves were used while handling nests and their contents. Human observer visitations to the nests did not affect nest predation rates in my study (see Appended Chapter A). Nests were considered successful if one or more young fledged after no losses to predators, and depredated if the nest failed completely due to predation (i.e. if eggs or nestlings younger than fledging age disappeared from the nest with definitive evidence of depredation).

For the purpose of analysis of daily survival rates, I only used nests that were confirmed as either successfully fledged or were confirmed lost to predators. These included: GP (L+A = 159 nests; L+B = 75 nests), YBP (L+A = 116 nests; L+B = 55 nests), and OTL (L+A = 82 nests; L+B = 58 nests). Daily nest predation rates were calculated using the Mayfield method (Mayfield 1961, 1975). Standard errors for Mayfield's daily predation probabilities were calculated as described by Hensler and Nichols (1981) and Johnson (1979). I separately analyzed nest survival rates for the incubation and nestling period.

Sony camcorders with 360x Digital zoom lenses were set up on tripods as low as possible at a distance of 3 – 5 m from nests to record parental activity during their incubation and nestling stages. All camcorders were placed in a well camouflaged hide. During the incubation stage, video recording were made on any day after the confirmed day of clutch completion. During the nestling period, all video recordings were made when the nestling were 9-10 days old, or one or two days after primary feathers broke their sheaths.

No nests were sampled more than once per nesting stage. Video recording was restricted to nests containing a clutch or brood size of three, this being the mean and modal size for all three species in my study area. Each videotaping season lasted six hours beginning at 07h00 and ending at 13h00. The number of feeding trips to and from the nest by both parents per hour were averaged over the six hours for each nest. This was then averaged across nests in order to obtain mean values for each species. At least six video samples (mean = 11 nests per species during incubation, and 23 nests per species during the nestling stage) were collected per species (Yellow-breasted Pipit, Orange-throated Longclaw, and Grassveld Pipit) in each of the two grassland management systems (i.e. L+A and L+B). A total of 203 nests were sampled in this way.

I tested for nest-site effects independent of parental activity by re-using natural nests of GP, YBP, and OTL during the 1999/2000 breeding season. For the purpose of this Chapter, only those nests confirmed as either successfully fledged or were confirmed lost to predators, were included. Natural nests were re-used as experimental nests two weeks after termination. These nests were divided into three categories based on their original outcome when there was parental activity: (a) nests that were depredated during the incubation stage, (b) nests that were depredated during the nestling stage, and (c) nests that successfully fledged young. I placed two eggs (a real Red Bishop *Euplectus orix* egg, and an artificial egg) in each of the experimental nests. Artificial eggs were made by filling natural eggs shells (donated by the Durban Natural Science Museum) with wax. The wax eggs simulated the 'host' species' eggs for both size and colour, while the real egg simulated the 'host' species' egg only for size. I left the two eggs (one real and one artificial) exposed to predators for 14 days (period equivalent to incubation stage for the study species), but monitored them using the same procedure as for naturally active nests. Gloves were used while handling both real and artificial eggs. I calculated daily predation rates for each of the three groups separately. This design allowed me to examine nest predation rates of experimental clutches relative to their prior natural fate.

I tested whether nest predation differed between nesting stages once nest-site effects were taken into account. This was done by considering experiments that removed effects of parental activity as the reference point for examining effects of parental activity according to Martin *et al.* (2000b). Briefly, species with small or no changes in parental activity between stages should show nest predation differences that are similar to those found in the experiments that removed effects of parental activity. If nest predation increases

proximately with an increase in parental activity, greater increases in parental activity should yield greater increases in nest predation relative to incubation, thereby offsetting the nest site effect. I tested for a positive correlation between the change in parental activity and nest predation based on the relative change in parental activity and predation between nesting stages. Changes in predation and activity levels between stages were calculated by subtracting incubation stage data from nestling stage data for both parental activity and predation data (see Martin *et al.* 2000b).

Differences in parental activity and daily predation rates between the incubation and nestling stages were tested using a paired *t*-test across the three species in order to explore general relationships. I compared daily predation rates using the program CONTRAST (Hines and Sauer 1989). Pearson moment product correlations was used for testing correlation between change in parental activity and nests predation across species.

RESULTS

Previously, I found that management practices affect nest predation rates in the study system (Chapter 2). To the ends, nest predation was significantly higher in grasslands under light grazing with infrequent burning, than those under light grazing, with frequent burning. I therefore, present my results on the two treatments separately.

Grassland under light grazing with infrequent burning

Parental activity (visits to the nests) across species was significantly greater during the nestling than during the incubation stage (14.2 ± 1.4 versus 3.0 ± 0.7 trips h^{-1}; Paired *t*-test, $t = 27.7$, 2df, $P < 0.001$), but individual species varied in the magnitude of relative differences in activity between stages (Fig. 1a). Daily predation rates were, however, not different between the incubation and nestling stages across species (0.06 ± 0.02 versus 0.05 ± 0.005; $P > 0.05$). However, within species daily predation rates varied for some species during both the incubation and nestling stages (Fig. 1b, Table 1).

When parental activity was controlled for (by re-using active natural nests with artificial clutches), daily nest predation rates differed significantly among the three nest outcome categories ($\chi^2 = 19.1$, df = 2, $P < 0.0001$). Nests that had a high risk of predation when used by active parents, had a correspondingly high predation risk when re-used as experimental nests (Fig. 2). Daily nest predation rate was higher in nests that were depredated during incubation, than nests that were previously successful (Fig. 2). Daily

nest predation rates were significantly higher for the experimental nests that were previously depredated during incubation (when parents were present) than experimental nests that were previously depredated during the nestling stage (i.e. when parent were present) ($\chi^2 = 8.6$, df = 1, $P < 0.003$).

When nest-site effects were removed, daily nest predation rates increased with a change in parental activity between stages both within and between species (Fig. 3; r = 0.95). GP, which showed the highest change in parental activity between stages, had the greatest increase in nest predation relative to incubation (Fig. 3).

Grassland under light grazing with frequent burning

Parental activity across species was significantly greater during the nestling than during the incubation stage (12.6 ± 2.9 versus 2.9 ± 0.5 trips h^{-1}; Paired *t*-test, $t = 8.2$, 2df, $P < 0.015$), but individual species varied in the magnitude of the relative differences between stages (Fig. 4a). Daily predation rates were not significantly different between incubation and nestling stages between species (0.03 ± 0.002 versus 0.02 ± 0.02, $P > 0.05$) and within species (Fig 4b, Table 2).

When parental activity was controlled for (by re-using active natural nests with artificial clutches), daily nest predation rates differed significantly among the three nest outcome categories ($\chi^2 = 8.3$, df = 2, $P < 0.02$). Nests that had a high risk of predation when used by active parents, had a correspondingly high predation risk when re-used as experimental nests (Fig. 5). Daily nest predation rate was higher in nests that were depredated during incubation than nests that were previously successful (Fig. 5). However, daily nest predation rates did not differ between the experimental nests that were previously depredated during incubation (when parents were present) and experimental nests that were previously depredated during the nestling stage (when parent were present) ($P > 0.05$).

When nest-site effects were removed, daily nest predation rates increased with parental activity both within and between species (Fig. 6; r = 0.99). This increase in nest predation was, however, proportional to the change in parental activity between stages. For example, GP, which had the highest change in parental activity between stages, showed the greatest increase in nest predation relative to incubation (Fig. 6).

Table 1. Comparison of daily predation rates (± SE) of natural nests during the incubation and nestling stages on annually burned grassland using the Mayfield method (1961, 1975).

Species	Incubation	Nestling	χ^2	df	*P*
Grassveld Pipit	0.038 (0.005)	0.042 (0.006)	0.31	1	0.58
Yellow-breasted Pipit	0.064 (0.008)	0.052 (0.008)	0.94	1	0.33
Orange-throated Longclaw	0.077 (0.012)	0.047 (0.009)	4.03	1	0.04

Table 2. Comparison of daily predation rates (± SE) of natural nests during the incubation and nestling stages on biennially burned grassland using the Mayfield method (1961, 1975).

Species	Incubation	Nestling	χ^2	df	*P*
Grassveld Pipit	0.025 (0.006)	0.041 (0.008)	2.48	1	0.12
Yellow-breasted Pipit	0.026 (0.007)	0.012 (0.004)	2.80	1	0.09
Orange-throated Longclaw	0.029 (0.008)	0.013 (0.006)	2.38	1	0.12

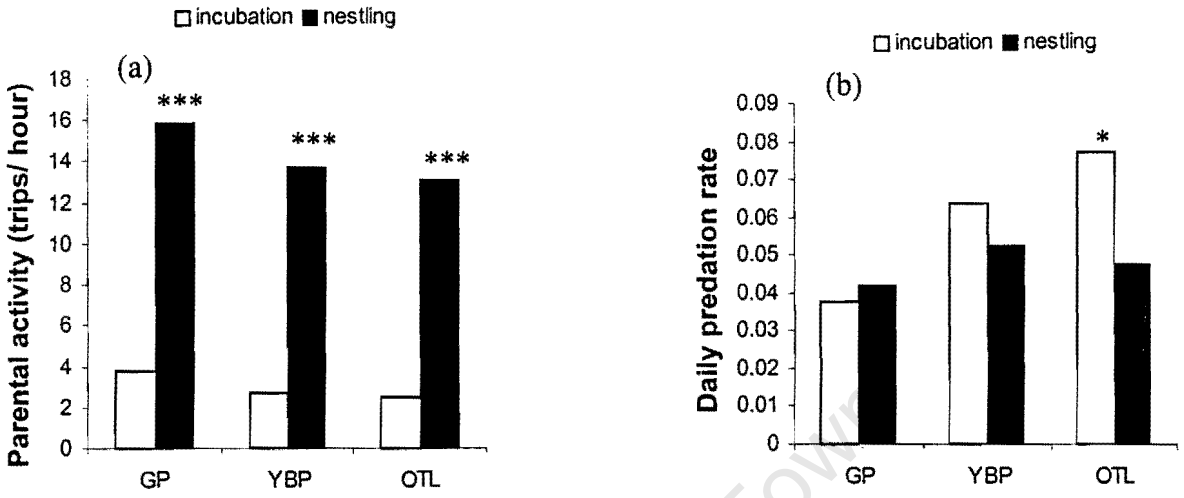

Fig. 1. (a) Parental activity (number of trips to and from the nest per hour) during the incubation and nestling stages of three ecologically similar grassland bird species nesting in annually burned grasslands. (b) Daily nest predation rates for the incubation and nestling stages. Species: GP – Grassveld Pipit; YBP – Yellow-breasted Pipit; OTL – Orange-throated Longclaw. Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. (Paired *t*-test, $P > 0.05$).

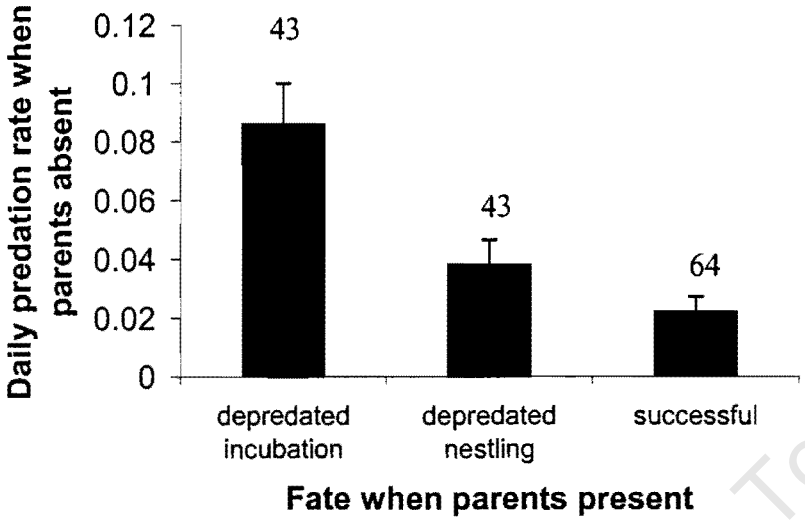

Fig.2. Daily predation rates (± SE) for three ecologically similar grassland bird species (Grassveld Pipit; Yellow-breasted Pipit and Orange-throated Longclaw) nests that were re-used with experimental clutches (a real Red bishop egg, and an artificial egg) on annually burned grasslands. The nests were grouped into three categories based on their original fate when parents were present (nests that were depredated during incubation stage, nests that were depredated during the nestling stage, and nests that successfully fledged young). Numbers above bars indicate the number of nests sampled.

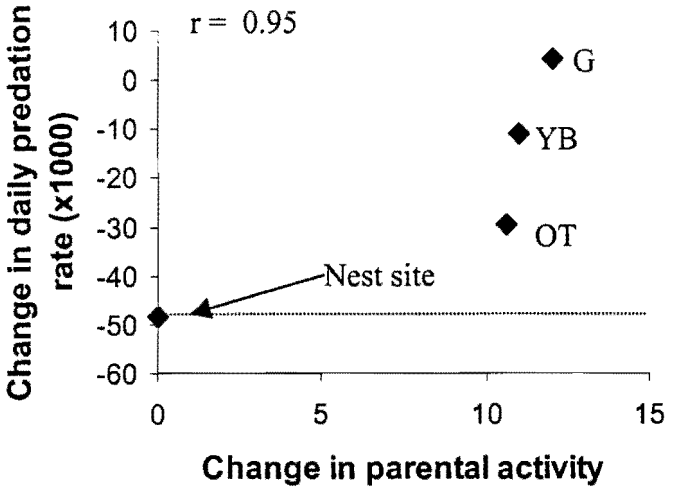

Fig.3. Correlation between the change in parental activity versus daily predation rates once nest-site effects were removed on annually burned grasslands (GP – Grassveld Pipit; YBP – Yellow-breasted Pipit and OTL – Orange-throated Longclaw).

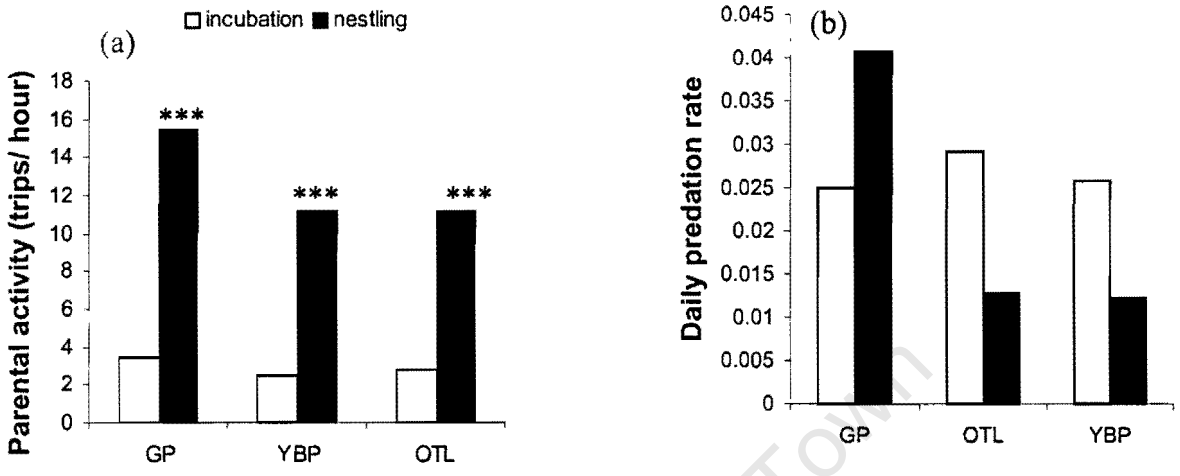

Fig. 4. (a) Parental activity (number of trips to and from the nest per hour) during the incubation and nestling stages of three ecologically similar grassland bird species nesting on biennially burned grasslands. (b) Daily nest predation rates for the incubation and nestling stages. Species: GP – Grassveld Pipit; YBP – Yellow-breasted Pipit; OTL – Orange-throated Longclaw. Asterisks indicate significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. (Paired *t*-test, $P > 0.05$).

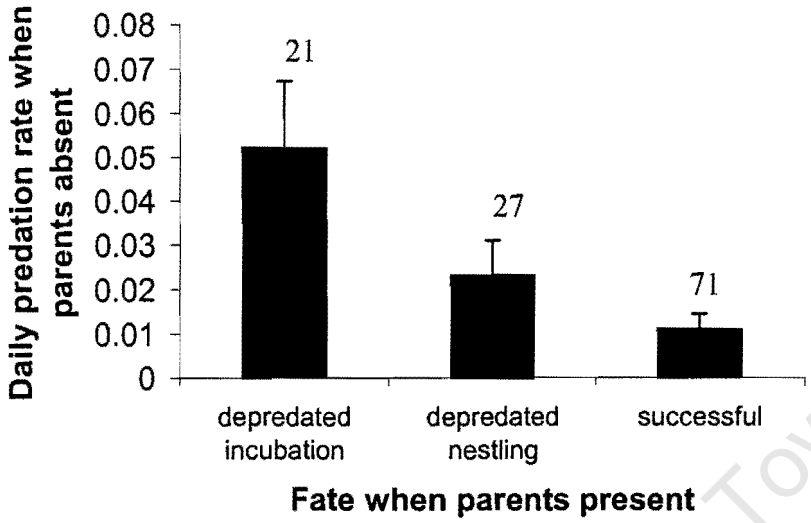

Fig.5. Daily predation rates (± SE) for three ecologically similar grassland bird species (Grassveld Pipit; Yellow-breasted Pipit and Orange-throated Longclaw) nests that were re-used with experimental clutches (a real Red bishop egg, and an artificial egg) on biennially burned grasslands. The nests were grouped into three categories based on their original fate when parents were present (nests that were depredated during incubation stage, nests that were depredated during the nestling stage, and nests that successfully fledged young). Numbers above bars indicate the number of nests sampled.

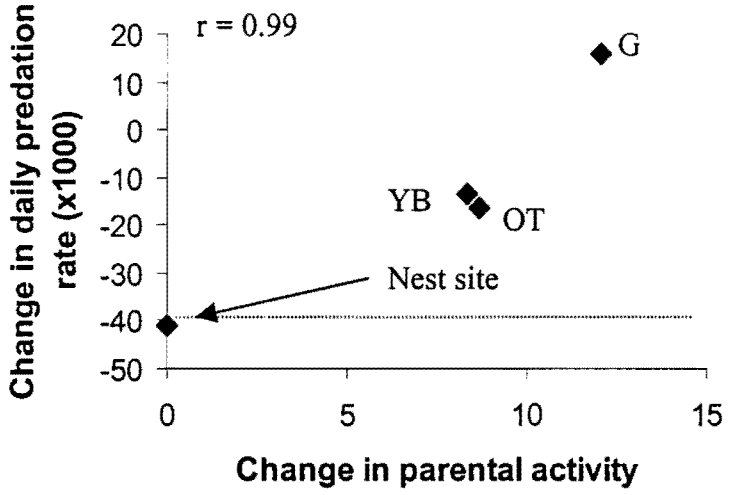

Fig.6. Correlation between the change in parental activity versus daily predation rates once nest site effects were removed on biennially burned grasslands (GP, Grassveld Pipit; YBP, Yellow-breasted Pipit and OTL, Orange-throated Longclaw).

DISCUSSION

Skutch (1949) hypothesized that higher nest predation constrains the rate at which parent birds can deliver food to young and thereby constrains clutch size by limiting the number of young that parents can feed. Skutch argued that predators are diurnal and they use parental activity to find nests. Surricates, which are diurnal, were among the most common mammalian predators in the present study. Snakes are also known to use a variety of visual stimuli including the intensity of parental mobbing behaviour to locate nests (Goodman and Goodman 1976, Czaplicki and Porter 1974). For such predators, increased activity at nests is expected to elevate nest predation during the nestling stage (when activity is greatest) compared to the incubation stage.

Alexander Skutch's (1949) hypothesis predicts that increased parental activity at the nest can proximately increase the risk of nest predation. Thus, one would expect a higher risk of predation during the nestling than the incubation phase. Without taking into account the effects of nest site, my results suggest that nest predation is generally not greater during the nestling than the incubation stage. Indeed, for OTL in annually burned grassland, nest predation was higher during the incubation than during the nestling stage. Similar results have been found by other studies (e.g. see Roper and Goldstein 1997, Lloyd 1998, Martin *et al.* 2000b). Superficially, one might be tempted to reject the Skutch hypothesis of parental activity and nest predation rates. However, nests that had a high risk of predation when used by active parents had a correspondingly high risk of predation when the same nests were re-used with artificial clutches – i.e. parents not present. This suggests that nest-site characteristics have a strong effect on nest predation risk. Thus, nest-site effects apparently can mask effects of parental activity on nest predation. Certainly, a careful consideration of there being no difference in predation rates between nesting stages can indicate a strong effect of parental activity balancing the opposing nest site effects in influencing nest predation (also see Martin *et al.* 2000b).

Nests most vulnerable to predators are likely to be found by predators early in the nesting cycle (i.e. during incubation); consequently, those that survive this period are likely to remain undetected. Nests in microhabitats with poor nest-site characteristics are thus expected to have higher predation rates during incubation than during the nestling stage, simply because of the effects of the nest site. Indeed, within patches that were both lightly grazed and annually burned (poor-quality nest-site microhabitat) (Chapter 2), there was a general trend towards an increasing vulnerability to predation risk during incubation than

during nestling stage for species that require greater nesting cover (i.e. YBP and OTL). This trend, however, disappeared in patches that were both lightly grazed and biennially burned (high-quality nest-site microhabitat) (Chapter 2).

Once nests-site effects were accounted for, nest predation increased with parental activity both within and between species. This supports Skutch's (1949) hypothesis of increased nest predation during the nestling period (when activity is greatest) compared to during incubation. This emphasises the need to effectively control for nest-site effects in studies testing Skutch's hypothesis (also see Martin *et al.* 2000b). My results are in accordance with other studies (e.g. see Martin et al. 2000b) and add support to the idea that increased parental activity at the nest can increase the risk of nest predation, but that nest-site effect first have to be properly controlled.

8

SYNTHESIS

South African grassland habitats and their management regimes

Natural and semi-natural grasslands occur extensively around the word. In South Africa they include low and high altitude grasslands. Although the distribution and maintenance of grasslands is primarily limited by the interplay between geography, soil type, altitude and climatic factors, the processes of grazing and fire often play fundamental roles. In South Africa, the grassland biome is under enormous pressure from agricultural development, afforestation, industrialization, mining, urbanization and degradation by intensive grazing and inappropriate use of fire (e.g. see Brooke 1984, Clancey 1985, Macdonald 1989, Low and Rebelo 1996, Cowling *et al.* 1997, O'Connor and Bredenkamp 1997). Despite this pressure, and the associated decline in bird populations (Clancey 1985, Keith *et al.* 1992, Tarboton 1997b), remarkably little is known about the avifauna of southern African grasslands, their ecology, and the manner in which they are affected by current land-use changes. Also, while the effects of fire and grazing pressure on the health of grassland ecosystems in terms of their capacity to support livestock is well understood, effects of these management practices on the natural biota is poorly known.

Effects of grazing intensity on recruitment

Comparison of vegetation characteristics showed more ground vegetation cover, greater foliage density, and greater heterogeneity on lightly grazed than heavily grazed grasslands (Chapter 2). This suggests that grazing affect vegetation, and consequently abundance or availability of food resources and nesting sites for breeding birds. Vegetation density and complexity have been shown to reflect the availability of both food and nest sites (Chapters 3, 4, 5 and 6). I suggest that the shift from wild to domestic grazing has drastically intensified the effect of grazing on grassland habitats and their associated fauna. Wild ungulates were nomadic or migratory, occurring infrequently at high density for short periods. Domestic livestock are present, usually at high densities, year-round.

The current intensive grazing pressure on the grasslands of South Africa affects bird abundance, distribution, species coexistence, breeding density, clutch initiation dates, duration of the breeding season and clutch size. Avian species diversity and abundance

could be limited by food availability and foraging efficiency, or by predation and availability of nesting resources (Chapters 2-7). Most birds were more than twice as abundant in lightly grazed than in heavily grazed grassland (Chapter 3). This study indicates that some species avoid nesting in heavily grazed grasslands although they forage there at low densities (Chapter 3). Further, management plans based on species abundance or presence without considering nest-site resources may be misleading and grazing affects bird populations through a reduction in nest-site availability and suitability, which in turn influences breeding success.

My results further clearly demonstrate that the general patterns of daily nest success rates are severely affected by grazing intensity. Daily nest survival is higher under light grazing than under heavy grazing pressure (Chapter 2). Grazing can also increase the abundance of predators (Martin 1992) and reduce alternate prey (Medin and Clary 1990), which can influence the overall level of predation risk. The frequency of predation may also vary with the species composition of nest predators (e.g. Norment 1993), which is also influenced by grazing (Martin 1992). One explanation for the higher mortality in heavily grazed grasslands is that nests are easier to locate by predators as a result of reduced cover there (Chapter 4 and 5). Cover can also influence the thermal environment of nests (Walsberg 1985). Birds in heavily stocked grasslands, where cover is generally less, are likely to occasionally leave the nest because of heat stress and consequently to leave their eggs or nestlings unattended.

The density of grassland vegetation can be important in determining the shading and concealment features of a habitat (Chapter 5). Nestlings that move out of the nests because of high temperatures (e.g. see Yorio and Boersma 1994) are also more vulnerable to predation because they might expose themselves to predators while seeking shade. Birds that fledge in heavily grazed grasslands could possibly behaviourally compensate for the cover condition of their nests. However, these compensation strategies may be energetically costly thus compromising future reproductive output. Persistent re-nesting after nest failure and consequent multiple brooding can, however, offset high nest mortality rates to some extent (Martin 1992). Such compensation may not be possible in heavily disturbed grassland systems where predation is prevalent throughout the breeding season.

I propose that grasslands should ideally be grazed moderately. It might be difficult to stop all undesirable management practices within a given region. One management approach to maintaining stable populations of grassland birds in disturbed habitats (e.g.

heavily grazed grasslands) where recruitment no longer matches mortality, is to intersperse poorly managed farms with appropriately managed ones. A single large grassland farm/farms grazed moderately at the scale of the management unit could act as a 'source' to compliment surrounding 'sink' farms. Overall productivity could then be enhanced because of the high density and nest success associated with the 'source' (see Pulliam 1988). The spacing of such 'source' versus sink' areas should be in such a way to allow normal dispersal. The spatial relationship among potential `source' and `sink' patches, and the consequences of source-sink dynamics, however, require further investigation.

Effects of fire frequency on recruitment

Grasslands managed under less frequent fires showed more ground vegetation cover, greater foliage density, and greater heterogeneity than under more frequent fires (Chapter 2). As expected, breeding commenced earlier in unburned grasslands than in annually burned grasslands (Chapter 3). This suggests that fire may affect the abundance or availability of nest-site resources. Birds breeding in frequently burned grasslands have to wait for vegetation to grow beyond a threshold before commencing with breeding. Early nesters are at an advantage as they potentially have a longer nesting season. In addition, the delay in clutch initiation is costly if seasonal declines in nesting conditions occur. A delay in clutch initiation reduces both the number of broods a successful pair can raise, as well as opportunities for re-nesting to replace depredated nests.

The most important impact that fire frequency has on recruitment is its effect on nesting success. My results clearly demonstrate that the general trend of daily success rates of nests is affected by fire frequency (Chapter 2). Daily nest survival is greatest under low fire frequency (Chapter 2). Frequent fires lead to the removal or reduction of nesting vegetation cover (Chapter 2), reduce nest concealment and make nests more visible to nest predators (Chapter 4 and 5). Dense vegetation can inhibit transmission of auditory or chemical stimuli (Chapter 5; also see Martin 1993c) and thus reduce vulnerability of nests to predation. If parents value their own survival (e.g. see Ghalambor and Martin 2001), particularly in areas where predation is intense, concealment provided by dense vegetation may contribute to the lower rate of nest abandonment by providing nesting parents with a greater sense of protection from predators. Superior cover may also improve nest macro- and microclimate, which may enhance nest survival (e.g. see Walsenberg 1985, Yorio and Boersma 1994). Frequent fires can also cause a reduction in diversity of nest-site

microhabitats and density of potential nest sites (Chapter 4). This in turn can then cause increased overlap in nest site use among coexisting species and, thereby increase nest predation (Chapter 4; also see Martin 1996a).

The low nest success that I recorded in the Wakkerstroom grasslands could well be below the level needed to balance mortality (Chapter 2). Indeed, nest success rates below 30% have been implicated in population declines in Neotropical migrants (Donovan *et al.* 1995) and shrubsteppe songbirds (Yanes and Suárez 1995). To enhance avian nesting success, management should be directed towards using appropriate fire frequencies. Ideally, the South African montane grasslands should be burned biennially. This maintains tall and dense growth which may restrict activity and search effort of nest predators and provide better nest concealment. The ideal management protocol should identify the most appropriate timing of burning, as well as the scale of the burn. However, further research is required to determine the trade-off between economic losses of livestock production and retention of grassland bird populations that might apply when farmers alter their management practices to benefit grassland birds.

Underlying mechanisms linking grassland bird population declines to grassland management practices

A major consequence of the most common management regime in South African grasslands (i.e. annual burning and heavy grazing) is reproductive failure among grassland birds. In particular, a regime of heavy grazing and annual burning increases grassland bird nest failure (Chapter 2). The main cause of nest failure is nest predation, regardless of grazing intensity, and accounts for > 87 % of the total nest failures (Chapter 2). Similarly, the major cause of nest mortality is nest predation regardless of fire frequency and together accounts for > 70 % of total nest failures (Chapter 2). The difference in the percentage of failure due to predation between management regimes suggests grazing affect nest predation more than fire. Failure due to other mortality factors was insignificant and did not differ between management regimes (Chapter 2). In addition, direct impacts of grazing and fire through removal of cover of active nests, disturbance of nests, or direct mortality through trampling and burning of nests are of little consequence (Chapter 2). Clearly these results support the hypothesis that potential demographic consequences of grazing and burning effects include altered susceptibility to reproductive failure, particularly as mediated through nest predation (e.g. see Ammon and Stacey 1997). It also suggests that

nest predation may be the proximate mechanism that drives bird population declines. Thus, management-practice mediated reproductive dysfunction via nest predation may be more important than food availability in regulating populations of the birds that live in South Africa's highland grassland ecosystems.

Can differences in life history explain variable responses by species to fire frequency and grazing intensity?

My study demonstrates a clear relationship between nesting success and management practices. There are, however, interspecific differences. For example, in the most widespread management regime (grassland managed under light grazing with frequent fires), Yellow-breasted Pipit (YBP) and Orange-throated Longclaw (OTL) both had similar levels of nesting success, whereas Grassveld Pipit (GP) was twice as successful. Nesting success for other species was variable.

In the following, I attempt to explain variable responses by species to fire frequency and grazing intensity. In particular, I examine the relationship between nesting success and a number of life history traits of the study species (Table 1) in order to identify life-history characteristics associated with nest survival. I focus my attention on the three ecologically similar grassland species of the family Motacillidae, viz. GP, YBP and OTL – in order to control for phylogeny. Only the GP was able to nest under heavy grazing (Chapter 2). The YBP and OTL require relatively more dense vegetation cover than GP for nesting and possibly hiding from danger while foraging. Species differences in nesting success can be explained in a couple of ways. First, nest placement, specificity in nest site selection, and predator specialization can explain species nesting success differences within treatments. For example, YBP and OTL showed higher nest-site specificity than the GP (Chapter 4). Search intensity of a nest predator may also increase with prey density (Martin 1988c). The degree of similarity of nest placement is high between YBP and OTL. Overlap or similarity of nest sites is assumed to incur a fitness cost (e.g. nest predation), because the resulting increase in cumulative nest density can increase density-dependent predation rates (Martin 1996a).

The generally higher mortality rate for YBP and OTL as compared to GP can possibly be explained by their plumage colouration. Birds with brighter plumage are easier to detect and thus face a higher risk of predation (e.g. see Anderson 1994). For those predators using behaviour and activity of parents as cues for detecting nests (Chapter 7),

Table 1. Reproductive characteristics and natural history of the focal birds species in the Wakkerstroom high-altitude grassland study area.

Species	Body mass (g)	Modal clutch size	Length of incubation period	Length of nestling period	Plumage colour	Type of nest	Residency	Status	Threat category
Grassveld Pipit	25	3	14 days	14 days	Brown	Cup-shaped	Altitudinal migrant	Common	None
Yellow-breasted Pipit	25	3	14 days	14 days	Yellow	Ball-shaped	Altitudinal migrant	Rare	Vulnerable
Orange-throated Longclaw	45	3	14 days	14 days	Yellow	Cup-shaped	resident	Common	None
Ayre's Cisticola	10	4	12 days	14 days	Brown	Ball-shaped	resident	Common	None
Long-tailed Window	35	3	14 days	16 days	Brown	Ball-shaped	resident	Common	None
Common Quail	120	6	19 days	precocial	Brown	Scrape on ground	Summer visitor	Common	None
Quail Finch	12	5	14 days	21 days	Brown	Ball-shaped	resident	Common	None
Rudd's Lark	20	3	14 days	14 days	Brown	Roofed Cup-shaped	resident	Rare	Critically endangered
Red-capped Lark	25	3	14 days	14 days	Brown	Cup-shaped	resident	Common	None

increased level of display as well as brightness of plumage of the parent are both factors that would increase conspicuousness – and thus vulnerability to predation (Goodman and Goodman 1976, Götmark & Hohlfalt 1994).

Egg colour can also contribute to the observed differences in species nesting success. A major function of egg colour is presumed to be protection from visually oriented predators (Oniki 1985), and egg colour is known to influence rates of predation (Yahner and Mahan 1996). The YBP and OTL generally lay creamy, white eggs, which may have been more conspicuous than the relatively brownish eggs of the GP. GP may also have adapted a kind of anti-predator defense response by concealing their eggs by means of back-ground matching of the cryptic nest colouration, a frequent kind of defense in birds (Ricklefs 1969). Egg size could explain the higher egg mortality experienced by OTL (Chapter 2). OTL nests are on average bigger than those of GP and YBP. Bigger eggs will require bigger nests and more cover for nest concealment (e.g. Møller 1990). If cover is limited, such nests will be more conspicuous increasing their vulnerability to nest predation. Another explanation is that, differences in nest predation between species could be due to the different anti-predator adaptations employed by the different species including mobbing, distraction displays, nest defense, nest guarding and reaction distances. Nest departure time and flushing distances are known to influence nest predation (Gochfield 1984, Byrkjedal 1987). GP adopts an anti-predator behaviour of sitting tight in the nest and only flushing within less than a meter, while the Long-tailed Widow (LTW) always sneaks away or flushes at a distance when approached by a predator (pers. obs.). Both these species have relatively high nesting success rates compared to others.

In addition to visual cues or activity at the nest, predators in grassland habitats may be locating nests by searching around the area from which birds have flushed. If this is so, one would expect reduced predation in denser vegetation. This was the case in my study (Chapter 2). This also suggests that it is likely to be easier for predators to locate nests during incubation than during the nestling phase because parents spend more time on the nest during incubation. In addition to nest-site effects (Chapter 7), such a mechanism can explain the lower predation during the nestling stage than incubation in OTL, YBP and Ayre's Cisticola (AC). This further supports the idea that the absence of adults from the nests can considerably reduce the risk of nest predation (Simon 1990). If predators locate nests by flushing birds from the nests, then the two anti-predatory behaviours as expressed by GP and LTW (see above), may indeed enhance nesting success for these two species.

Flushing distance and flushing decisions by OTL and YBP, particularly in grasslands with relatively little cover, may subject them to a higher risk of predation than that experienced by, for example, the GP.

Species-related variation in the intensity of begging and conspicuousness of the nestlings can also account for an increased likelihood of predation. To this end, OTL and YBP nestlings generally had their mouths open most of the time, while GP nestlings only opened theirs on presentation of food. Both OTL and YBP nestlings begged more when I disturbed the nest or when parents approached the nest than GP nestlings (from video observations). Begging activity is known to influence the risk of predation (Skutch 1949), with noisier nestlings being more vulnerable (Redondo and Castro 1992).

Open cup-shaped nest types were generally more vulnerable to predation than roofed nests. The differences in nest type could explain the generally higher nesting success among AC, Quail Finch and LTW – all of which build dome-shaped nests.

Residency throughout the year, for example in OTL, may enable birds to: (1) acquire knowledge, experience and familiarity with the habitat and with predator activity in the environs of the nest; (2) retain the same territory and mate during successive breeding attempts or between seasons, or (3) gain site dominance over others by remaining in the breeding site. All these factors are predicted to enhance survival. The hypothesis that long-term residency enhances nest survival (Robins *et al.* 1989), however, is not supported in this study. The GP, despite being a partial migrant, experienced markedly higher nesting success than the resident OTL. Indeed OTL (resident) and YBP (altitudinal migrant) experienced similar nest mortality suggesting that breeding success may not be related to the breeding pair's knowledge of the habitat or predators. Rather, nest-site selection itself is paramount in determining reproductive success.

Nesting success of the rare YBP in the most widespread management regime (grassland managed under light grazing with frequent fires) was similar to its closely related common congener, OTL, but half that of its other commonly occurring congener, the GP. Irrespective of phylogeny, rare species (YBP and Rudd's Lark), however, generally experience lower nest success than commoner species suggesting that they are more sensitive to management effects. The generally low nesting success rates for rare species may result from a combination of many life history characteristics that cumulatively and additively reduce nesting success.

Ecological constraints of nest predation and its influence on the evolution of avian life-histories

I was able to show that there was no observer effect within my study system (see Appended Chapter A). Thus, I have confidence in believing that it is the variables under examination that affected nest predation rates in my study.

In Chapter 7, I explicitly demonstrated that once nest-site effects are removed, nest predation increases with parental activity during the nestling stage within and between species. Further nest-site effects and parental activity apparently have additive effects on nest predation rates (Chapter 7). The increase in nest predation due to parental activity effects could influence the selection of nest-site choices (Chapter 4). The relationship between parental activity and nest predation should favour a negative evolutionary outcome (e.g. see Martin and Ghalambor 1999), where species nesting in areas with substantial risk of nest predation are expected to show trends towards reduced parental activity (e.g. Skutch 1949, Conway and Martin 2000). The relationship between parental activity and nest predation also supports the concept that nest predation places a critical evolutionary constraint on variation in avian clutch sizes (see Skutch 1949, Lima 1987, Linden and Moller 1989, Martin *et al.* 2000a). Large clutches should require more feeding trips by parents to the nest, thus placing the nest contents at greater risk from predators (Skutch 1949, Martin *et al.* 2000a). Consistently high nest predation such as that recorded in this study (Chapter 2) can then constrain the rate at which parent birds visit nests to feed their young (e.g. see Skutch 1949, Ghalambor and Martin 2001), thereby ultimately constraining clutch size by limiting food delivery. Lastly, the effects of parental activity on predation rates can place an important evolutionary constraint on variation in feeding rates and foraging strategies among species (Chapter 6), which can affect nestling growth rates and body condition of the chicks.

My results on parental activity (Chapter 7), and the tests of predictions of the nest predation (Skutch 1949), and food limitation hypotheses (Lack 1947) in determining optimal clutch size (Chapter 3), suggest that Lack's model of food limitation on clutch size could be rejected in favour of Skutch's hypothesis. Even though other factors may explain variation in clutch size, there is good reason to believe that nest predation is the most important factor driving the evolution of clutch size in my grassland study area.

Implication for conservation

The implications of my results (Chapter 2-6) for the management of grassland bird species are quite clear. To enhance nesting success and productivity of the focal study species, and grassland birds in general, management should focus on manipulating, increasing and maintaining habitat features that increase reproductive success as these have direct fitness consequences. I propose that grasslands should be managed according to the model depicted in Figure 1. Because risk of nest predation is affected by habitat characteristics at the scale of nest-site and nest-patch scale, (Chapter 5) grassland management should focus on improving habitat condition, particularly availability and suitability of nest sites, based on habitat attributes surrounding nests at a range of scales.

Although the total bird diversity and density was reduced by frequent burning and intense grazing, individual species were variously affected by different management practices (Chapter 2 and 3). These observations suggest that conservation planners should adopt an approach that considers individual species, or management for habitat mosaics for the conservation of multiple species. In order to benefit a diversity of birds, and the concern for conservation for a broad spectrum of species (e.g. see Ball *et al.* 1994, Maddock and Du Plessis 1999), managers should provide fine-scale diversity of vegetation characteristics within grazing fields. Based on habitat measurements and the reported classification functions (Chapter 4), managers can now easily predict the species likely to utilize a given plot. Such knowledge will assist in designing appropriate habitat manipulations for species of conservation concern. The richness of the regional avifauna will be maintained through availability of the full mosaic of habitat necessary for each species. The diversity of management practices, species and their habitat requirements are assumed to complicate effective management. However, the general similarity in the effects of management regimes across all species (Chapter 2 and 3), overlap of nest-sites (Chapter 4), and similarity of major habitat features determining nesting success across species (Chapter 4 and 6) suggest that grassland management practices and restoration programs for single priority species (Yellow-breasted Pipit for example), should provide habitat for a diversity of similar species.

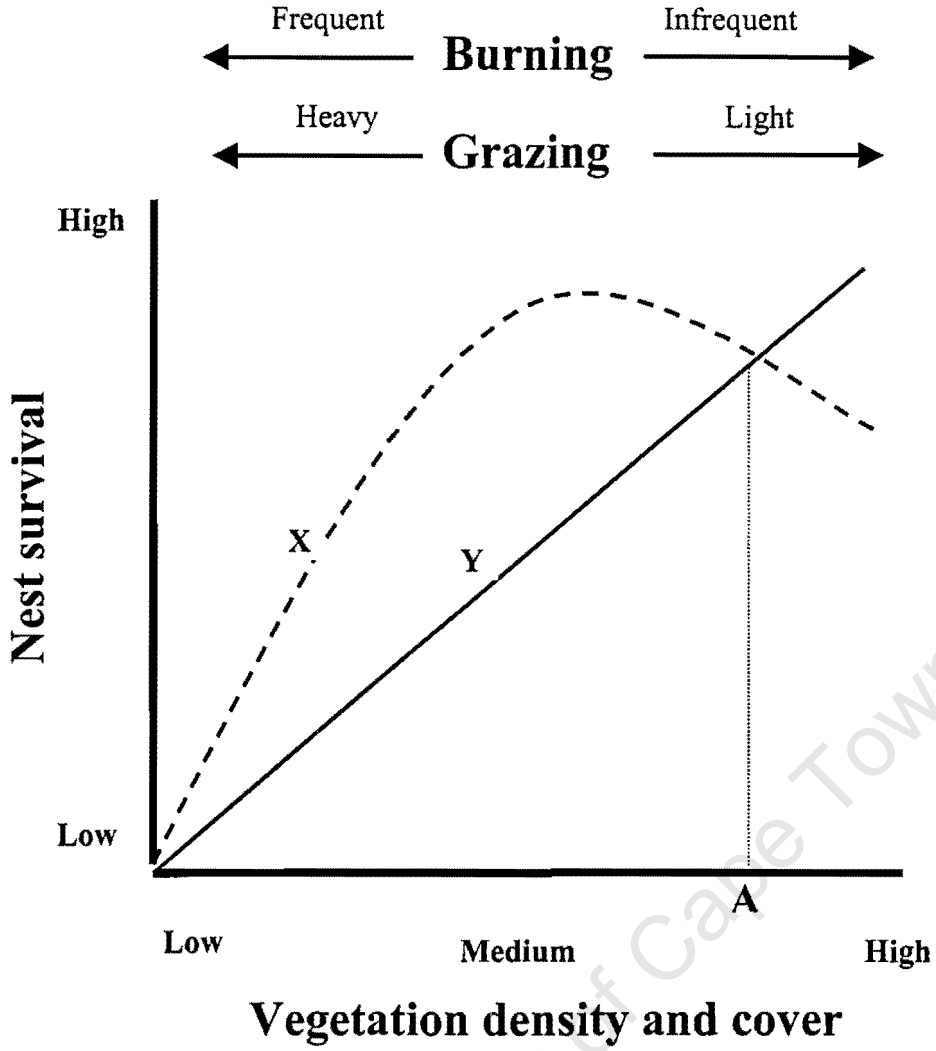

Fig 1. A simplified model linking management practices to nest survival of birds in the South African grasslands. The dotted line (X) represents food availability, while the solid line (Y) represents nest predation. Bear in mind that highest nest predation results in lowest nest survival, and vice versa. Point A indicates an hypothetically optimal trade-off between fire frequency and grazing pressure. The effects of nest predation would appear to outweigh those of food in determining general survival for grassland species. Thus, management should be biased towards maximizing areas for successful nesting, rather than foraging.

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Appendix A

Observer visitation to nests does not affect risk of nest predation in grassland system

Abstract

Estimates of nesting success are vital in studies of avian populations. To estimate nesting success, observers usually visit nests periodically to monitor nest contents. Regular visits to nests by observers can affect (increase or reduce) nesting success, particularly predation rates, which may yield biased and misleading conclusions regarding population viability. I examined whether regular researcher visits to the nests affected nest predation for eight grassland bird species breeding in high altitude grasslands of Wakkerstroom, South Africa. I found that investigator visit to the nests and visitation schedule did not affect nesting. This suggests that observers did not provide predators with cues for finding nests, and that frequent visits to nests have no cumulative effect on the probability of nest predation.

INTRODUCTION

Estimates of nesting success are important for the study of avian population dynamics, particularly for grassland birds, which usually suffer high levels of nest predation (Chapter 2). To determine nesting success, observers usually visit nests periodically to monitor nest contents (Mayfield 1961, 1975). The disturbance associated with regular nest visit by observers may positively or negatively affect the success of a sample of nests under observation (Bart and Robson 1982, Major 1990, Götmark 1992, Mayer-Goss *et al.* 1997, Lloyd 1998, Rotella *et al.* 2000). This can be manifested through the following: (1) predator following or being repelled by the observers scent and tracks to a nest (Bowen *et al.* 1976, Mayer-Goss *et al.* 1997); (2) displaced parents leaving the nest unattended (Westmoreland and Best 1985); and (3) attraction of predators to the nest either by the presence of an observer, or by the accompanied distraction and alarm behaviour of the displaced parents (Götmark *et al.*, 1990, 1992), or by nest re-location markers (Greenwood and Surgeant 1985). According to Rotella *et al.* (2000), estimates of nesting success can be strongly affected by even small observer effects, and may yield biased and misleading conclusions about variables under examination and inferences regarding population viability. Here, I test the hypothesis that visits to the nests by observers affect (increase or reduce) predation rates in my study.

Study species

My study focussed on eight ground-nesting grassland birds, viz. Yellow-breasted Pipit *Hemimacronyx* (*Anthus*) *chloris* (YBP), Grassveld Pipit *Anthus cinamomerous* (GP), Orange-throated Longclaw *Macrony capensis* (OTL), Ayres' Cisticola *Cisticola ayressii* (AC), Long-tailed Widow *Euplectes progne* (LTW), Common Quail *Coturnix coturnix* (CQ), and Quail Finch *Ortygospiza atricollis* (QF) and Rudd's Lark *Heteromirafa ruddii* (RL), Red-capped *Calandrella cinerea* Lark (RCL).

METHODS

Study area

The study was conducted in the high altitude grasslands of Wakkerstroom (centred at 27° 10' S, 30° 06' E) in Mpumalanga province, South Africa from 1998-2001. These grasslands are managed in three ways, viz. heavily grazed and annually burned (H+A), lightly grazed and annually burned (L+A), and lightly grazed and biennially burned (L+B). Vegetation varies considerably across management regimes with respect to floristics, vegetation cover, density, and structural heterogeneity. Birds generally avoided H+A for breeding purposes. I identified major predators through examining the nest and nest environs, examining the remains, marks in artificial wax eggs, baited traps, video cameras and direct observation. The main predators included snakes, foxes, mongooses, mice, shrews, and birds of prey (appendix 1). In the absence of predator identity from video evidence, snakes were identified as predators of natural nests when either of the following happened: crushed shells were found near the nest, eggs or nestling disappeared one or two at a time, and a dead nestling was found in or outside the nest with no apparent injury. Otherwise mammals were assumed to be the predators if broken eggs shells were found, nests severely damaged, torn out or removed, or there were bite marks on feathers.

Nest searches and monitoring

Study plots were searched for nests of all grassland bird species over the entire breeding season (October to April) during each of the years between 1998 and 2001. Searching and locating of nests was done by dragging a 50 m rope between two observers to flush out birds from nests, or based on behavioural observation. Nest sites were marked (for relocating) with a stick or stone placed 10 m away from each nest. Nests were monitored

over intervals of 1-6 days (rechecking intervals). I grouped my data set into rechecking interval lengths of 1, 2, 3, 4, 5, and 6 days for each nest. I recorded number of nests observed for each interval and the number of these observations that survived the interval. I only used nests that were confirmed as either successfully fledged, or were confirmed lost to predators for the purpose of analysis of observer effect. A total of 1202 nests were monitored over the three breeding seasons from 1998 through 2001. For the purpose of this chapter, I only used nests that were definitely exclusively lost to predation and those that fledged successfully (1084 in total). These nests yielded survival data for a total of 3031 intervals of 1-6 days. These data only include intervals in which the nest was successful or losses of nests were attributable to predators; losses due to other causes of mortality are not included here.

DATA ANALYSIS

To examine the importance of observer effects on the nesting success of study species across management, I used the maximum-likelihood estimator model (observer effect model) that estimates observer effect on daily survival rate for sets of data with observations from an array of rechecking or visitation-interval lengths (Rotella *et al.* 2000). In this model the probability of surviving an interval of t_i days between observations is: $P(\delta_i = 1 / t_i) = h*p^{ti}$, where P is the probability that a nest survives natural mortality each day; δ_i is an indicator variable that takes on the value of 1 if the nest survives an interval, and 0 otherwise; and h is the observer effect on the survival probability that occurs shortly after a nest visit. Values of h ranges between $h < 1$ and $h > 1$. If $h < 1$, observer visitation reduces risk of nest predation shortly after a nest visit. If $h > 1$,observer visitation increases risk of nest predation shortly after a nest visit. $h= 1$ shows no observer effect.

RESULTS AND DISCUSSION

There was no observer effect in my study system. Nest visits did not affect nesting success in all of the species. Observer effect model, h, was equal to 1.0 ($h = 1$) in each of the species in L+B grassland (Table 1). Observer effect model, h, ranged between 0.78 to 1.03 in L+A grassland (Table 2).

These results suggest that the disturbance associated with regular nest visits by observers in my study do not affect their outcome. Nest predation, the major cause of nesting failure for many passerine birds, did not increase in response to researcher

disturbance. Other studies have failed to detect any observer effect despite a widely held belief that predators, particularly mammals, would pose great threat to nests visited by researchers (see Götmark 1992, Lloyd 1988). Although serious effort should be made not to unnecessarily disturb nests, serious biases on fate of nests under observation are unlikely, and general visits to the nests by researchers working in grasslands in South Africa should not affect the validity of the information gathered.

Table 1. The number of nests in each interval found surviving (S_i) and depredated (F_i) and daily survival probability (p) and observer effect (h) of species in lightly grazed, but annually burned areas as calculated following Rotella *et al.* method (2000). Values of h ranges between $h<1$ and $h>1$. Values of $h < 1$ show that observer visitation reduces risk of nest predation shortly after a nest visit. If $h > 1$, observer visitation increases risk of nest predation shortly after a nest visit. Values of $h = 1$ shows no observer effect.

Species	Interval 1		Interval 2		Interval 3		Interval 4		Interval 5		Interval 6		Daily Survival Probability	Observer Effect (h)
Species	**S1**	**F1**	**S2**	**F2**	**S3**	**F3**	**S4**	**F4**	**S5**	**F5**	**S6**	**F6**		
Ayre's Cisticola	81	6	120	11	162	19	76	16	34	3	44	6	0.983	0.942
Common Quail	4	1	7	3	8	2	7	1	5	1	1	1	1.000	0.781
Long-tailed Widow	31	1	96	8	65	10	38	9	12	6	15	3	0.945	1.028
Orange-throated Longclaw	91	7	121	14	83	18	49	6	15	4	18	6	0.963	0.961
Grassveld Pipit	146	4	201	16	216	33	132	25	60	13	71	14	0.958	1.009
Yellow-breasted Pipit	146	13	223	23	138	25	84	20	32	5	36	10	0.966	0.956

Table 2. The number of nests in each interval found surviving (S_i) and depredated (F_i) and daily survival probability (p) and observer effect (h) of species in lightly grazed, but biennially burned areas as calculated following Rotella *et al.* method (2000). Values of h ranges between $h<1$ and $h>1$. Values of $h < 1$ show that observer visitation reduces risk of nest predation shortly after a nest visit. If $h > 1$, observer visitation increases risk of nest predation shortly after a nest visit. Values of $h = 1$ shows no observer effect.

Species	Interval 1		Interval 2		Interval 3		Interval 4		Interval 5		Interval 6		Daily Survival Probability	Observer Effect (h)
	S1	F1	S2	F2	S3	F3	S4	F4	S5	F5	S6	F6		
Ayre's Cisticola	20	1	46	2	21	1	28	4	31	3	24	1	0.991	0.964
Long-tailed Widow	33	1	86	9	72	6	56	6	37	5	57	7	0.987	0.950
Orange-throated Longclaw	33	1	82	5	79	4	57	6	28	2	38	4	0.987	0.976
Quail Finch	3	1	22	1	13	1	23	2	8	2	6	2	0.978	0.962
Grassveld Pipit	70	1	139	9	84	13	70	2	42	7	31	2	0.981	0.983
Yellow-breasted Pipit	45	1	105	6	86	5	47	4	40	1	22	2	0.993	0.967

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Appendix 1

Major potential nest predators identified (marked with asterisk*) and or found in and around the study area.

Mammals

Least dwarf shrew *Suncus infinitesimus*,
Greater Musk Shrew *Crocidura flavescens*,
*Rock Elephant Shrew *Elephantulus myurus*,
Lesser Savanna Doormouse *Graphiurus parvus*,
Sloggett's Rat *Otomys sloggetti*,
*Striped Mouse *Rhabdomys pumilio*,
House Mouse *Mus* musculus,
Natal Multimammate Mouse Astomys *natalensis*,
Highveld Gerbille *Atera brantsii*,
White-tailed Mouse *Mystromys albicaudatus*,
Grey Climbing Mouse *Dendromus melanotis*,
Aardwolf *Proteles cristatus*,
Caracal *Felis caracal*,
African Wild Cat *Felis lybica*,
Serval *Felis serval*,
*Cape Fox *Vulpes chama*,
*Black-backed Jackal *Canis mesomelas*,
African Weasel *Poecilogale albinucha*,
Striped Polecat *Ictonys striatus*,
Small-spotted Genet *Genetta genetta*,
Large-spotted Genet *Genetta tigrina*,
*Suricate *Suricata suricatta*,
*Yellow Mongoose *Cynictis penicillata*,
Slender Mongoose *Galerella sanguinea*,
White-tailed Mongoose *Ichneumia albicauda*,

Snakes

Natal Purple-glossed Snake *Amblyodipsas concolor*,
Common Purple-glossed Snake *Amblyodipsas polylepis*,
Brown House Snake* *Lamprophis fuliginosus*,
Olive House snake *Lamprophis inornatus*,
Spotted House Snake L*lamprophis guttatus*,
Aurora House Snake *Lamprophis aurora*,
Yellow-bellied House snake *Lamprophis fuscus*,
Cape Wolf Snake *Lycophidion capense*,
Variegated Wolf Snake *Lycophidion variegatum*,
Cape File Snake *Mehelya capensis*,
Mole Snake *Pseudaspis cana*,
Many-spotted Snake *Amplorhinus multimaculatus*,
*Rhombic Skaapsteker, *Psammophylax rhombeatus*,
Striped Skaapsteker *Psammophylax tritaeniatus*,
Short-snouted Grass Snake *Psammophis brevirostris*,
*Snout Grass Snake,
*Montane Grass Snake,
*Olive Grass Snake,
Sross-marked Grass Snake *Psammophis crucifer*,
*Rhombic Egg Eater *Dasypeltis scabra*,
Southern Brown Egg Eater *Dasypeltis inornata*,
Red-lipped Snake (herlad) *Crotophopeltis hotamboeia*,
Boomslang *Dispholidus typus*,
Spotted Harlequin Snake *Homoroselaps lacteus*,
Striped Harlequin Snake *Homoroselaps dorsalis*,
Sundevall's Garter Snake *Elapsoidea sunderwalli*,
Mozambique Spitting Cobra *Naja mossambica*,
*Rinkhals *Hemachatus haemachatus*,
Rhombic Night Adder *Causus rhombeatus*,
*Puffadder *Bitis arietans*,
Berg Adder *Bitis atropos*,

Birds

* Fiscal Shrike*Lanius collaris*,
*Staneley's Bustand *Neotis denhami*,
*Red-cheasted Sparrow Hawk *Accipiter rufiventris*,